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REGIONAL VARIATION IN THE NORTH AMERICAN ELEMENTS OF *OXALIS* *CORNICULATA* (OXALIDACEAE)

Billie L. Turner

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

The native North American elements of *Oxalis corniculata* L. are treated within two infraspecific groupings: var. *pilosa* (Nutt. ex Torr. & Gray) B.L. Turner, *comb. nov.*, and var. *wrightii* (A. Gray) B.L. Turner, *comb. nov.* These appear to be the only meaningful naturally occurring populational segregates in North America, the former variety occurring mostly in the drier more elevated portions of western U.S.A., México, and Central America, the latter occurring mostly in the grassland regions of central U.S.A. from Canada to the Mexican border. A syndrome of characters serve to distinguish the taxa, for which a key is constructed and a map showing their distribution is provided.

KEY WORDS: Oxalidaceae, *Oxalis*, Texas, México

The North American yellow flowered species of *Oxalis* belonging to the section *Corniculatae* DC. (namely *O. corniculata* L. and its close relatives) are extremely difficult taxonomically and have been the subject of much discussion and nomenclatural confusion. Wiegand (1925) provided a rather detailed overview of the North American elements of the *O. corniculata* complex, recognizing in this ten species, some of these with several varieties, most of the latter lacking morphogeographic integrity. Shinnery (1956) provided a treatment of *O. dillenii* Jacq. (*sensu* Eiten 1955) for Texas. In this he recognized a needless new variety, *O. d.* var. *radicans* Shinnery, and *O. d.* var. *dillenii*. I consider both of these to be the same as my concept of *O. corniculata* var. *wrightii* (A. Gray) B.L. Turner. Shinnery also recognized a "dark green creeping plant with brownish, oblong stipules, occurs as a rather recent introduction in southern Texas ..." as *O. corniculata*, but I cannot distinguish most of the latter from *O. c.* var. *wrightii*, although I would not deny the existence of an occasional introductant of *O. c.* var. *corniculata* *sensu* Lourteig (*cf.* below).

Eiten (1963) presented a broad imaginative world-wide synthetic treatment of sect. *Corniculatae* in which its two subsections, *Strictae* Eiten and *Corniculatae*, were thought to have developed early on in Eurasia, the former migrating to North America, the latter to South America, these subsequently expanding their territories in the New World, so much so that the two sections reestablished a secondary contact in North America, presumably in México to judge from his Figure 2 showing ancestral migratory pathways in the group. In spite of its breadth and imaginative tone, Eiten (1963, p. 241) considered his taxonomic treatment to be no more than a "synopsis", providing only partial synonymy for most of the nineteen taxa (fourteen species and five subspecies) recognized. His was a conservative treatment; he proposed no new species and attempted to recognize morphogeographic elements within some of the more widespread species, calling these subspecies. He provided a detailed key to the various taxa, according to continent. In North America (including Central America and the West Indies) he recognized fourteen species, several of these with infraspecific taxa. Unfortunately, some of the more widespread elements of this complex were inadequately typified, as noted by Lourteig (1979) in her comprehensive taxonomic account of sect. *Corniculatae* for extra South American elements. In this ambitious treatment she recognized twelve species as native to North America, providing a nearly complete synonymy with detailed citation of specimens documenting distribution. In terms of nomenclature, her major contribution was that of the typification of *O. stricta* L. vis-a-vis *O. corniculata* and *O. dillenii*, a subject touched upon in some detail much earlier by Eiten (1955).

My interest in all of the above has to do with the names applicable to populations of *Oxalis corniculata* in México and Texas, especially the latter. Both Eiten and Lourteig used subspecific categories for their major morphogeographical elements within this species. Eiten, however, regarded *O. corniculata* as largely an Old World element, albeit "A universal weed in all inhabited regions except the Arctic." Adding "In that part of North America which is north of Mexico in the west, and north of the immediately Gulf Coast in the east, the species is apparently confined to gardens, lawns and greenhouses." For those elements of *O. corniculata* (sensu Lourteig 1979) he took up the name *O. albicans* H.B.K.; for most of the central and eastern U.S.A. material of this complex he took up the names *O. dillenii* and *O. stricta*.

Lourteig, hopefully after resolving problems in typification, recognized *Oxalis corniculata* as a largely pantropical element, lectotypified by an Old World collection made by Thunberg (Lourteig 1979, p. 60). Consequently, in her treatment, while maintaining most of the taxa accepted by Eiten, she modified the nomenclature to reflect her study. Within the *O. corniculata* complex touched upon by Eiten, this included: 1) recognition of *Oxalis corniculata* as native to North America; 2) elevation of *O. albicans* subsp. *californica* (Abrams) Eiten to specific rank (as was earlier accorded the taxon by other

workers); 3) recognition of *O. albicans* subsp. *pilosa* (Nutt. ex Torr. & Gray) Eiten as a subsp. of *O. corniculata*; 4) recognition of *O. albicans* subsp. *albicans* as a subsp. of *O. corniculata*; and 5) *O. dillenii* Jacq. as a synonym of *O. stricta* (which will not further concern us here).

As might be inferred from the above, if one accepts Lourteig's concept of *Oxalis corniculata* as a worldwide largely pantropical species, there appear to be 2 or 3 infraspecific elements in North America: 1) subsp. *corniculata*, a poorly defined element having mostly purely yellow petals said by Lourteig to occur throughout much of temperate North America (perhaps where introduced, but not so indicated by Lourteig), but more so throughout México and Central America; 2) subsp. *albicans*, which is typified by material from the west coast of central México and said to differ from subsp. *corniculata* (with which it is sympatric) in possessing orangish-yellow petals and a thicker more ligneous tap-root, which seems to be the case, but certainly many of the citations of subsp. *corniculata* given by Lourteig in her treatment (e.g., TEXAS: Bejar Co., *Berlandier* 152, 1810 [F]; and Hidalgo Co., *Painter & Barkley* 14470 [TEX!]) must reflect ignorance as to flower color or else these are atypical elements of her subsp. *albicans*; and 3) subsp. *pilosa*, said to be a relatively localized taxon of the drier regions of northcentral México and closely adjacent U.S.A. (with what appear to be a few misidentifications from more remote areas pitched in), typified by material from southern California.

Lourteig has provided an informative Figure 6 illustrating representative plants of subsp. *albicans* and subsp. *pilosa*, and the characters enumerated by her in key and description form appear to be diagnostic, as a *syndrome*. I emphasize the latter because in my examination of 500 or more sheets of this complex from México and adjacent U.S.A., exceptions to this or that character state are found in individuals and/or populations throughout the region concerned. Nevertheless, I do find regional validity of those two complexes as morphogeographical intergrading entities deserving of nomenclatural recognition, but at the varietal level, which is in keeping with at least most current practice in North America, if not elsewhere. Because of this I find it expedient to propose the following new combinations for the North American elements of *Oxalis corniculata*:

OXALIS CORNICULATA L. var. **WRIGHTII** (A. Gray) B.L. Turner,
comb. nov. BASIONYM: *Oxalis wrightii* A. Gray, *Pl. Wright.* 1:27.
1852.

This taxon is typified by material collected by Charles Wright, probably in New Mexico (GH!). Its salient features are well depicted in Figure 6a of Lourteig (as subsp. *albicans*). Lourteig took up the subspecific name *albicans* for this taxon, but its earliest name at the varietal level occurred when *Oxalis*

wrightii A. Gray var. *pilosa* (Nutt. ex Torr. & Gray) Wiegand was first proposed in 1925, the varietal epithet *wrightii* being automatically formed at that time under the current *International Code of Botanical Nomenclature*. The general distribution of var. *wrightii* vis-a-vis var. *pilosa* is shown in Figure 1. As will be noted, I view var. *wrightii* as mostly a taxon of the central U.S.A., intergrading at about the Mexican border into the more widespread, more variable var. *pilosa*.

It should be noted that many current authors apparently have recognized two species from among my concept of *Oxalis corniculata* var. *wrightii*. McGregor (1979) in his treatment of *Oxalis* for the Great Plains Flora recognized two sympatric species within the *O. corniculata* complex, *O. dillenii* Jacq. and *O. stricta* L. He did not recognize *O. corniculata*, but the latter two taxa apparently both apply to what I have called *O. corniculata* var. *wrightii*. He distinguished *O. stricta* by pubescence type, largely following the work of Eiten (1963). I could also have recognized two such names but, at least in Texas, these appear to be but pubescence forms of a single taxon which I have called *O. c.* var. *wrightii*, following the biology of Lourteig (1979), who typifies and restricted *O. stricta* to the more eastern portions of the U.S.A., extending westward to about the easternmost limits of *O. c.* var. *wrightii*.

OXALIS CORNICULATA L. var. PILOSA (Nutt. ex Torr. & Gray) B.L.

Turner, *comb. nov.*, BASIONYM: *Oxalis pilosa* Nutt. ex Torr. & Gray, *Fl. N. Amer.* 1:212. 1838.

This taxon is typified by material collected by Nuttall in California. Its salient features are depicted in Figure 6b of Lourteig (as subsp. *pilosa*). Lourteig took up the subspecific name *pilosa* for this taxon but its earliest name at the varietal level occurred autonymically with the combination *O. pilosa* var. *subpilosa* (Wiegand) Wiegand, first proposed in 1926, heterotypic with var. *pilosa*.

The following key to these two North American varietal taxa should help identify typical elements of each. I cannot distinguish Lourteig's subsp. *pilosa* from her subsp. *albicans* in México and have applied the name var. *pilosa* to nearly all of the specimens in this region (Figure 2), including specimens she cites as subsp. *corniculata* (although probable but occasional introduced elements of the latter need not be denied).

1. Sepals mostly 2.5-3.5 mm long, rather evenly pubescent throughout; apices of sepals mostly obtuse or rounded, weakly tufted if at all; peduncles with mostly appressed hairs; stems erect, arising from slender rhizomes; central U.S.A. to the Mexican border (Figure 1). var. *wrightii*

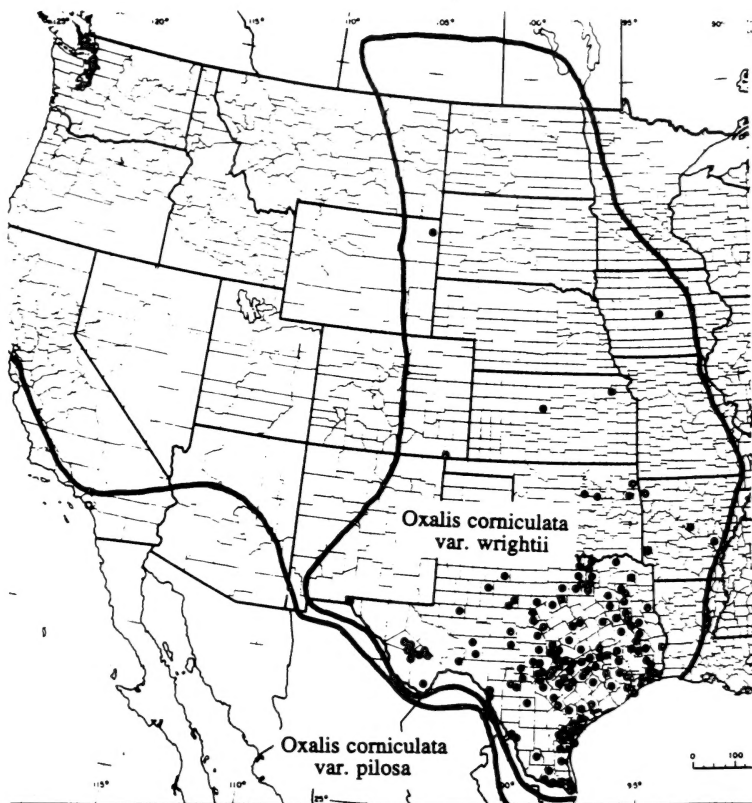


Figure 1. Approximate distribution of *Oxalis corniculata* var. *wrightii* in North America. Circles indicate collections of this taxon annotated and on file at LL, TEX. This variety intergrades into var. *pilosa* along a band of about 200 km along the U.S.A.-México border, mainly in México.

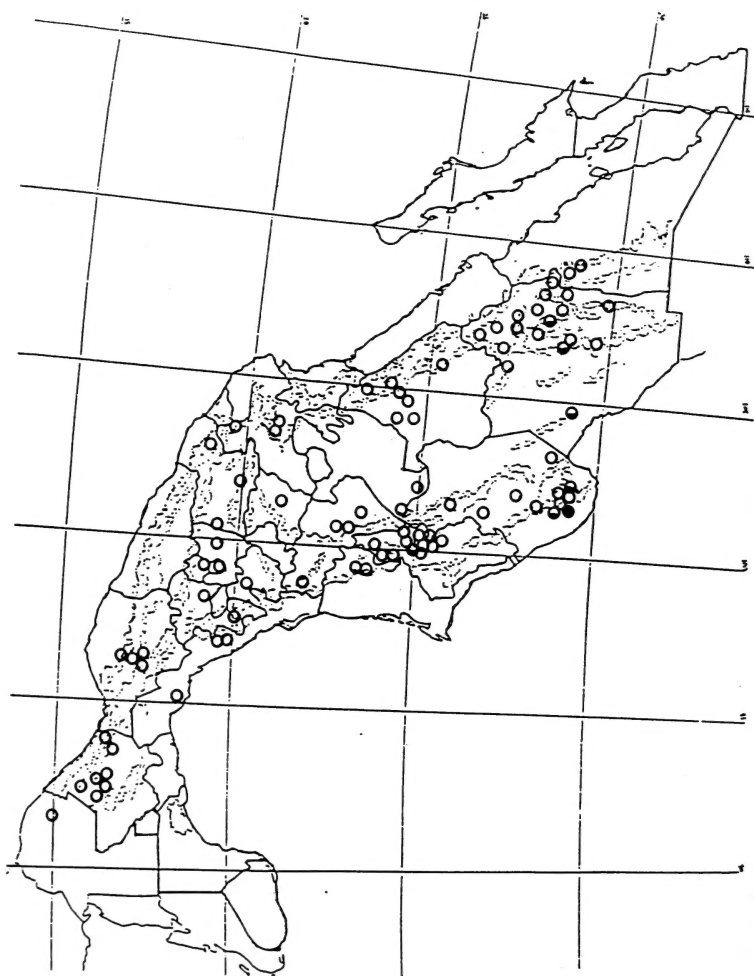


Figure 2. Distribution of *Oxalis corniculata* var. *pilosa* in México (open circles), var. *wrightii* (closed circles), and \pm intermediates (half-shaded circles). Annotated specimens vouchering this distribution are on file at LL, TEX.

1. Sepals mostly 3.5-6.0 mm long, partially glabrate or unevenly pubescent; apices of sepals mostly acute, tufted; peduncles with mostly spreading hairs; stems usually procumbent, arising from ligneous thickened root-stocks, or not; western U.S.A. and throughout México. var. *pilosa*

It should be reiterated that the several characters (from among a syndrome) listed in the above key are quite variable and each is much prone to environmental modification as well as genetic perturbation. Considering the exceptional variability of the *Oxalis corniculata* species complex one might well ask the question: need infraspecific taxa be recognized at all? Perhaps not, but where morphogeographical elements seem reasonably well defined, as in the case of var. *wrightii*, I see no good reason not to. Perhaps future workers with more field work will be able to subdivide *O. corniculata* (s.l.) into meaningful infraspecific groupings with more certainty.

ACKNOWLEDGMENTS

This study is based upon the examination of approximately 500 sheets at LL, TEX, mostly from Texas and México. I am grateful to Guy Nesom and Piero Delprete for helpful suggestions in reviewing the paper.

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PERSPECTIVA HISTORICA DE LA CLASIFICACION DE LA FAMILIA POACEAE

Yolanda Herrera Arrieta¹

CIIDIR Unidad Durango, Instituto Politécnico Nacional, Apartado Postal
738, Durango, Dgo., C.P. 34000 MEXICO

RESUMEN

La clasificación de la familia Poaceae se ha modificado a través del tiempo en concordancia con la evolución del conocimiento de la familia y el progreso del desarrollo científico. Los caracteres morfológicos regían los primeros sistemas de clasificación. Más tarde, otro tipo de caracteres adquieren importancia, lo que conlleva a una mejor comprensión de las unidades biológicas. Así, a los objetivos iniciales de generar un sistema de clasificación sencillo, confiable y reproducible se ha agregado el de explicar las relaciones filogenéticas de las entidades, a fin de encontrar un sistema de clasificación que refleje la dinámica de cambio en las especies biológicas.

Según el criterio de la mayoría de los agrostólogos del mundo, los caracteres anatómicos sumados a los morfológicos y respaldos por su información cromosómica, dieron como resultado bases taxonómicas de gran valor para separar subfamilias y tribus dentro de las Poaceas. La información bioquímica, escasa por el momento, parece promisoría para la interpretación de las relaciones y las tendencias evolutivas de esta familia, especialmente a nivel infraespecífico. A la fecha, parece ser que existe un consenso generalizado entre los agrostólogos en cuanto a la división subfamiliar de las Poaceas. Sin embargo, todavía existen problemas que requieren solución en la división tribal, especialmente en los grupos periféricos.

SUMMARY

The classification of the Poaceae has been modified as the evolutionary knowledge of the family has progressed with scientific developments and resulting treatments. The primary classification system

¹Becaria de a COFAA

was based on morphological characters which distinguished the family. Later, other descriptors were incorporated to resolve the difficult systematics of this family in order to gain a better understanding of the biological ultrastructure. In addition to the initial goals of providing a classification system that is simple, reliable, and reproducible, the interpretation of the species relationships must be incorporated into a phylogenetic classification system which reflects the changing biology of the species.

The criteria as proposed by agrostologists demand that anatomical characters and chromosomal data must be combined with the morphological features to provide a valuable and comprehensive taxonomic base that will clarify and in so doing, bring about a logical separation of the family into subfamilies and tribes. Biochemical information on the family is scarce today. However, it seems to be a promising approach that will aid in the interpretation of relationships and indicate evolutionary trends in the family, especially at the infraspecific level. Nowadays, there is a general agreement among agrostologists on the division of the Poaceae into subfamilies. However, problems which require resolution, start at the tribal level, specifically in the peripheral groups.

PALABRAS CLAVES: Paper review, revisión histórica, Gramineae, Poaceae

INTRODUCCION

Las Poaceas (gramíneas) constituyen una de las más grandes familias de plantas vasculares en el mundo, con cerca de 620 géneros y casi 10,000 especies (Clayton & Renvoize 1986). Ocupan el tercer lugar después de las orquídeas y de las compuestas, considerando su número de géneros; y el cuatro lugar después de las orquídeas, las compuestas, y las leguminosas, considerando su número de especies. Es, sin embargo, la familia más importante en términos económicos y muy probablemente la más ampliamente distribuida. Los pastizales son comunidades naturales compuestas principalmente de gramíneas, las cuales ocupan un tercio de la superficie de la Tierra (Shantz 1954). Los cereales, tan importantes en la dieta alimenticia de la población del mundo, son también gramíneas. Por su importancia, el estudio de las gramíneas va mas allá de la mera satisfacción de una simple curiosidad acerca de la diversidad de las cosas vivas (Stebbins 1956). Los genetistas del maíz, caña de azúcar y en general de los cereales han aprendido que muchas especies de pastos silvestres están bastante relacionadas con los cereales y forrajes cultivados. Las prácticas de cruzamiento e hibridación iniciadas por Mendel en el siglo XIX estan orientadas en trabajos recientes a incluir genes extra que le confieran a

la planta características como: vigor; la elevación del contenido proteínico del grano; resistencia a enfermedades y plagas, a sequía y heladas, a condiciones desfavorables del suelo, etc.

Se han hecho varias propuestas de clasificación de las gramíneas en los diferentes niveles (subfamiliar y tribal) de acuerdo al avance tecnológico y a la filosofía prevalente en el momento histórico.

En esta revisión bibliográfica, se presentan y comparan los diversos sistemas de clasificación que se han propuesto para las gramíneas, dada su caracterización general según la época y sus diversas aproximaciones filosóficas y metodológicas. El propósito es presentar los cambios más significativos que se han hecho en la clasificación de las gramíneas (familia Poaceae), como un ejemplo tangible de los cambios en la sistemática de las plantas. Así pues, el objetivo de esta revisión histórica de la familia Poaceae es presentar los cambios en su clasificación, como ejemplo para ilustrar los sistemas taxonómicos de plantas que se emplean actualmente.

TRATAMIENTO TAXONOMICO

Por su importancia económica, las gramíneas fueron uno de los primeros grupos de plantas que recibieron nombre y fueron colocados en categorías especiales, resultado del deseo natural del hombre por diferenciar aquellas con las que tenía contacto. Así, la clasificación temprana de plantas evolucionó hacia lo que más tarde alcanzó a ser la Taxonomía. Theophrastus concretó el primer esfuerzo para conocer las plantas 300 años antes de la Era Cristiana. Sin embargo, fue hasta el siglo XVIII que se publicaron los trabajos de Linneo *Species Plantarum* (1753), los que marcaron el punto de partida de la nomenclatura binomial de las plantas vasculares, cuyo objetivo único fue desarrollar un método para identificar de una manera sencilla y reproducible la variedad de plantas conocidas en su tiempo, producto de las exploraciones geográficas de los siglos anteriores. Durante el siglo XIX, se efectuó un cambio substancial en los objetivos de clasificar las plantas, agrupándolas por características morfológicas similares. A este sistema se le denominó clasificación natural. Brown (1810) y posteriormente Beauvois (1812, citados en Prat 1936) fueron los primeros en reconocer las espiguillas como caracteres fundamentales para separar especies de gramíneas. Brown estableció dos grandes subdivisiones de las gramíneas: las panicoides y las pooides y su división se basa en las siguientes diferencias (Cuadro #1).

Durante el segundo y tercer cuarto del siglo XIX continuaron las discrepancias en el modo de clasificar las gramíneas, período en el que la búsqueda de caracteres confiables parecía ser la gran tarea. Los factores que afectaron la precisión de las clasificaciones en ese tiempo fueron las limitaciones en comunicación, lo que no permitía el acceso a plantas de otros lugares y a la

CUADRO #1. Clasificación de Brown (1810).

Espiguilla pooide	Espiguilla panicoide
-comprimida lateralmente	-comprimida dorsalmente
-desarticulada arriba de las glumas	-desarticulada abajo de las glumas
-la raquilla extendida arriba de la flor superior	-la raquilla finaliza en la flor superior

información de estudios florísticos realizados en áreas relativamente lejanas. Hubo algunos agrostólogos que propusieron la división subfamiliar basandose en el carácter de la separación de sexos, obviamente sin éxito, dada la gran incidencia de hermafroditismo y lo azaroso del monoicismo y dioicismo en los pastos. Elias Fris (citado en Fournier 1878) propuso dividir las en dos grandes series: *Eryanthae*, aquellas cuya flor se abre y *Clisanthe* en las que la flor no se abre durante la antesis, carácter difícilmente aplicable por ser momentáneo y fugaz. Otros autores dividieron la familia con base en la naturaleza de la espiguilla: *Lacustiflorae*, aquellos que llevan las flores perfectas en la extremidad, como en las *Paniceae* y *Spiculiflorae*, las que la llevan en la base, como en las *Poaceae* (Fournier 1878). Este autor en un trabajo que es interesante mencionar por tener la característica de haber reunido 643 especies de gramíneas mexicanas, número impresionante para su tiempo, propone la división de la familia con base en la simetría de la espiguilla en relación al eje principal; su propuesta tampoco fue muy exitosa.

Fue hasta 1881 cuando Bentham (citado en Auquier 1963) publicó un trabajo notable en la clasificación de la familia *Poaceae*, basado en observaciones originales de las características morfológicas de la inflorescencia de un gran número de pastos provenientes de Europa, Hong Kong, Australia, América, y Africa; como también a través de las ideas de Munro (de su trabajo con plantas de la India y Australia), a quien dió reconocimiento. La clasificación de Bentham se resume en el Cuadro # 2 que se muestra a continuación.

Hackel publicó en 1887 (citado en Barkworth 1992) un tratado de las gramíneas muy similar al de Bentham.

Las subfamilias y tribus de Bentham y Hackel han sido aceptadas durante mucho tiempo por los agrostólogos americanos, y fueron prácticamente adoptadas por A.S. Hitchcock quien en 1935 publicó su *Manual of Grasses for the United States of America*, basado en el sistema de Bentham. Entre las escasas modificaciones que Hitchcock hizo a este sistema, encontramos que las tribus *Oryzeae* y *Zoysieae* fueron transferidas a la subfamilia *Festucoideae* (*Pooideae*) y la pequeña entidad *Zizanieae* que Bentham consideraba parte de *Oryzeae* fue elevada al rango de tribu. El *Manual* de Hitchcock ha sido considerado como

CUADRO #2. Clasificación de Bentham (1881).

Subfamilias: PANICOIDEAE FESTUCOIDEAE		
Tribus:	Paniceae	Bambuseae
	Andropogoneae	Festuceae
	Tripsaceae	Hordeae
	Melinideae	Aveneae
	Zoysieae	Agrostideae
	Oryzeae	Chlorideae
		Phalarideae

un tratado básico de las gramíneas de Norte América y se le encuentra citado en la mayoría de los estudios ecológicos y taxonómicos de los pastizales de dicha región.

TRATAMIENTO SISTEMICO

El problema de delimitar especies en los pastizales de América no fue totalmente resuelto con el uso del *Manual* de Hitchcock, ni aún cuando recurrimos al uso de monografías o floras regionales, dificultades que experimentan todavía los especialistas al tratar de definir las entidades biológicas. Darwin señaló el fin de la taxonomía como una ciencia puramente descriptiva con su publicación *The Origin of Species*, en 1859, donde se establecen las bases del concepto de especie biológica.

Los genetistas establecieron las razones más importantes para definir el concepto de especie (aunque el problema no se ha simplificado) cuando se visualizaron los procesos de hibridación natural y doblamiento de cromosomas o poliploidía, procesos sumamente frecuentes en plantas. Poniendo en claro con ello que las "especies" son el resultado temporal de toda una red de interacciones entre tres, cuatro o más ancestros, juntos, separados o aun divergentes en su distribución (Stebbins 1956).

En el segundo cuarto del siglo XX, los métodos de los botánicos empezaron a presentar una transición gradual hacia una epistemología taxonómica de la teoría evolutiva, con el objeto de llegar a una comprensión completa de la Teoría de Selección Natural y las Leyes de la Herencia. Huxley, Anderson, Stebbins, Clausen, y Grant, entre otros, sentaron los fundamentos intelectuales y procedimientos para una nueva aproximación. Los taxónomos de este tiempo empezaron a adoptar aproximaciones filogenéticas en la taxonomía de las plantas.

Stebbins (1956) hace notar que las inflorescencias de las gramíneas son caracteres menos confiables como indicadores de las tendencias evolutivas que

las inflorescencias de otras familias tales como Rosaceae, Ranunculaceae, o Liliaceae. El uso de los caracteres morfológicos de la inflorescencia de las gramíneas como indicadores de sus tendencias evolutivas presenta un número de inconveniencias que se resumen en: 1) La gran reducción de tamaño y complejidad de sus partes reproductivas limita la calidad taxonómica de sus caracteres, mientras que en otras familias son de gran ayuda (Stebbins 1982); 2) Se tienen indicios de evolución paralela muy frecuentemente en la familia (Decker 1964; Renvoize 1981; Estes & Tylr 1982). Aunado a lo anterior, dos aspectos comunes como son la hibridación o fecundación cruzada (causante de poliploidia y apomixis) y la autofecundación oscurecen los límites taxonómicos y hacen difícil aplicar el concepto de especie biológica en muchas gramíneas (Campbell 1985).

Por todas estas dificultades los agrostólogos del siglo presente han desarrollado investigaciones en forma intensiva para encontrar características indicadoras mas confiables que aquellas que han sido comunmente usadas en los sistemas tradicionales, a fin de clasificar y relacionar genética y evolutivamente el grupo tan especial que son las gramíneas. Muchos otros caracteres han sido encontrados y poco a poco se han ido incorporando en esta difícil tarea, como son: la anatomía de las hojas, la estructura del embrión y de los granos de almidón en la cariósida; también algunos caracteres aparte de los morfológicos como son el tamaño de los cromosomas y su número básico, la fisiología de fijación de carbano, similitudes inmunológicas de las proteínas; y finalmente la información molecular que se vienen generando en las investigaciones de la última década, como la variación de isoenzimas y la secuencia del Acido Desoxiribonucleico (ADN).

Los acontecimientos que afectaron profundamente el curso de la biosistemática de pastos y de las plantas en general fueron los hallazgos de Duval-Jouve (1870 y 1875) y Pee-Laby (1898), (entre otros mencionados en Prat 1936), anatomistas que empezaron a analizar y comprar las hojas de las gramíneas bajo el microscopio, encontrando todo un mosaico de caracteres en la epidermis y en el corte transversal de las hojas. Duval-Jouve es considerado el padre de la anatomía sistemática de la familia. Los taxónomos de ese tiempo, no prestaron atención a los caracteres encontrados por los anatomistas, sino hasta el tiempo en que apareció el primer trabajo importante del citólogo ruso Avdulov (1931, citado en Prat 1936) *Investigaciones Cariotaxonómicas de la Familia de las Gramíneas*, quien llamó la atención al proporcionar un sistema de clasificación con base en el número y tamaño de los cromosomas de 232 pastos analizados, sistema que él mismo enfatizó era muy similar al que resultaba de los caracteres anatómicos e histológicos de las hojas, e igualmente diferente al sistema tradicional de Bentham.

Prat (1932), anatomista francés, enfatizó la importancia de la epidermis de las hojas en la clasificación de las gramíneas. Cuatro años más tarde (1936) este autor agrupó las gramíneas en tres subfamilias: Festucoideae, Panicoideae,

y Bambusoideae con base en la correlación entre los caracteres anatómicos y la epidermis de las hojas. Los trabajos de Avdulov y de Prat dieron las bases para la redefinición de las pooides, de donde se sustrajo el grupo de pastos chloridoides. Este grupo había sido tratado tradicionalmente como parte de las pooides por los caracteres morfológicos de sus espiguillas, pero los nuevos caracteres encontrados demostraron claramente su relación más próxima a las panicoides. Para encontrar información taxonómica nueva y la incorporación de ésta en el establecimiento de las relaciones subfamiliares las investigaciones subsecuentes han sido altamente productivas. Como resultado de ello se han generado varios sistemas modernos de clasificación que serán presentados a continuación.

I. Clasificación a nivel de subfamilia.

Entre 1956 y 1966 se propusieron sistemas nuevos de clasificación de las Poaceae, en los cuales se incorporó información derivada de caracteres crípticos (no reconocidos) en adición a los atributos más tradicionales. La mayoría de estos sistemas reconocieron más de las dos subfamilias (Panicoideae y Festucoideae) por lo general aceptadas anteriormente. Se reconocieron de cuatro a doce subfamilias o grupos equivalentes como resultado de los estudios de estos nuevos caracteres (Watson *et al.* 1985). Un intento notable de reagrupamiento fue el de Stebbins (1956), quien propuso la primera división en cuatro grupos: Panicoideae, Chloridoideae, Festucoideae, y Bambusoideae, basado en la combinación de varios caracteres crípticos como la anatomía foliar, número y tamaño de cromosomas, forma de plántulas, epidermis foliar, lodículos, cariósido, embrión y estructura de las espiguillas. El mismo autor propuso un posible origen tropical de las gramíneas con base en la retención de caracteres primitivos en la epidermis de las hojas, cariósido, embrión y plántulas de grupos poco especializados dentro de la familia. Trabajos subsecuentes han demostrado que el nivel más sorprendente de congruencias a nivel supragenérico de los taxa proviene de la información de fuentes anatómicas, citogenéticas y del embrión, según Campbell (1985).

La circunscripción precisa de las subfamilias se está clarificando en los intentos actuales de sintetizar los conocimientos alcanzados y todavía se requiere de la asignación satisfactoria de varios géneros dentro de esta "estructura."

Ellis (1987) presenta un resumen de las características que definen las subfamilias vistas como principales líneas de evolución, consideradas en general, en las clasificaciones propuestas por Renvoize (1981), Clifford & Watson (1977), Watson & Dallwitz (1980), and Watson *et al.* (1985).

Hasta 1985, y durante los últimos 20 años, se han establecido en cinco subfamilias, con algunas diferencias menores en el tratamiento de grupos pequeños, ejemplo de ello son los tratados de: Renvoize (1981), Campbell (1985), y Wat-

CUADRO #3.

Subfamilia	Tribus	Tribus perifericas
BAMBUSOIDEAE	Arundinarieae	Brachylytreae
	Oryzeae	Diarrheneae
	Phareae	Stipeae
ARUNDINOIDEAE	Aristideae	
	Arundineae	
	Centothecaeae	
POOIDEAE	Agrostoidaeae	
	Aveneae	
	Meliceae	
	Poeae	
	Bromeae	
	Triticeae	
CHLORIDOIDEAE	Aeluropodeae	
	Cynodontaeae	
	Unioleae	
	Zoysiaeae	
PANICOIDEAE	Andropogoneae	
	Paniceae	

son *et al.* (1985). El Cuadro #3 resume los grupos aceptados por Campbell (1985) para el Sureste de los Estados Unidos.

Clayton & Renvoize en 1986 presentaron el más completo recuento de la familia Poaceae, proporcionando descripciones claras de las subfamilias y tribus. Las diferencias que estos autores presentan en su análisis de la familia con respecto a los trabajos anteriores son de índole variada; incluyen grupos adicionales que no habían sido considerados, otros que son nuevos para la ciencia, así como un análisis cladístico con una aproximación clara de las relaciones filogenéticas entre los taxa. Son seis las subfamilias propuestas por ellos: Bambusoideae, Pooideae, Centothecoideae (Centostecoideae), Arundinoideae, Chloridoideae, y Panicoideae. La diferencia en este nivel consiste en aceptar el criterio de Soderstrom (1981) de elevar a nivel de subfamilia a las Centothecaeas.

II. Clasificación Tribal.

La clasificación subfamiliar de mayor aceptación entre los agrostólogos modernos parece ser aquella de cinco subfamilias: Pooideae, Bambusoideae, Arundinoideae, Chloridoideae, y Panicoideae; división que fue propuesta, como se mencionó antes, por Clifford & Watson (1977), Watson & Dallwitz (1980), y Watson *et al* (1985). Este sistema se basa principalmente en caracteres embriológicos y anatómicos de las hojas. Clayton & Renvoize (1986) presentan descripciones muy completas de las subfamilias, en las que resumen los rasgos que las caracterizan, resultado de casi un siglo de investigaciones.

No se puede decir que exista un consenso general para la división de la familia al nivel de tribu, especialistas en las diferentes subfamilias se encuentran trabajando arduamente para lograr presentar bases firmes en la división tribal, de ellos podemos mencionar a Soderstrom & Ellis (1987) en las Bambusoideae; Macfarlane (1987) en las Pooideae; y a Conert (1987) en las Arundinoideae.

Como se puede ver hasta aquí, los estudios anatómicos han sido muy productivos en relación a la clasificación supragenérica de la familia Poaceae; sin embargo, en trabajos recientes otro tipo de metodologías están siendo utilizadas para investigar la biosistemática de las gramíneas. Ejemplos de ello se presentan a continuación.

DIVERSIDAD BIOQUIMICA EN POACEAE

Una problema que enfrenta con frecuencia el procesamiento de la información generada del estudio morfológico de un grupo de plantas muy emparentadas, es el que se refiere a la estabilidad de los caracteres utilizados en la clasificación del grupo. A menudo se ha encontrado que las condiciones ambientales modifican o determinan ciertas características morfológicas de las plantas. Por esta razón los taxónomos se han dado a la tarea de encontrar otro tipo de caracteres que pudieran ser más estables, es decir con menor plasticidad genética. Los caracteres bioquímicos, a diferencia de los caracteres morfológicos son en general más confiables. Estos se dividen en caracteres micromoleculares y macromoleculares, los primeros están, como los caracteres morfológicos, también sujetos a los factores ambientales, lo que les hace manifestarse de diferente manera en hábitats diversos; mientras que los segundos, se presume que son de mayor confiabilidad ya que se caracterizan directamente a partir del genotipo (ADN).

Los estudios de variación fitoquímica micromolecular que han sido empleados con mayor frecuencia en la sistemática de plantas, son el contenido de los flavonoides, terpenoides, y alcaloides. De éstos, solamente los flavonoides se presentan en las gramíneas. Son muchísimas las plantas que se han caracterizado a la fecha en base al contenido de flavonoides. Harborne (1988), por

ejemplo, resume por familia los compuestos químicos determinados en cientos de trabajos aislados. Los resultados de la evaluación del perfil de flavonoides en pastos ha sido fructífera solamente a nivel genérico e infragenérico a la fecha. Parece ser que la química de los flavonoides en las poaceas no ha sido estudiada suficientemente para permitir hacer generalizaciones a partir de esta fuente de datos. Este panorama seguramente cambiará en el futuro con la acumulación de información en esta área de estudio.

Un ejemplo de utilización del perfil de flavonoides en gramíneas es el realizado por Herrera & Bain (1991) y Herrera & Grant (1993), quienes investigaron las probables relaciones filogenéticas entre las especies del complejo llamado *Muhlenbergia montana* (Nutt.) Hitchc. Estos autores señalaron una especie como posible ancestro del grupo, confirmaron un caso de hibridación entre dos especies con caracteres morfológicos intermedios, indentificaron un caso de relación infraespecífica entre dos taxa con nivel conocido de especie y encontraron que el proceso de evolución química del grupo no fue congruente con el proceso de evolución morfológica.

Los estudios macromoleculares sobre el contenido proteico que se han realizado con fines sistémicos, emplean diversas metodologías como son: comparaciones serológicas, patrones de variación de proteínas, contenido de aloenzimas e isoenzimas; y muy recientemente varias técnicas de caracterización del ADN. Se presentan a continuación algunos ejemplos de estas metodologías aplicadas a las gramíneas.

Las técnicas serológicas se basan en las reacciones de antígeno-anticuerpo mostradas por los mamíferos ante la presencia de proteínas extrañas a las del organismo. Los estudios serológicos no implican la identificación de las proteínas ni el conocimiento de sus funciones. Esta ventaja ha hecho que en la actualidad sea una técnica poco utilizada.

De los escasos estudios serológicos que se han realizado con gramíneas es importante mencionar el reportado por Esen & Hilu (1989), quienes investigaron las afinidades inmunológicas entre las subfamilias de las Poaceae. Estos autores incluyeron 22 taxa provenientes de las subfamilias Pooideae, Chloridoideae, Panicoideae, Arundinoideae, y Bambusoideae. Encontraron que la información inmunológica revela una posible tendencia evolutiva de los pastos, en forma muy estrecha en los grupos chloridoide y panicoide, por una parte y en las bambusoides y las arundinoides por otro. Los resultados también subrayan la heterogeneidad de los taxa dentro de las Pooideae.

La estructura y diversidad de la prolamina en las Poaceae es un ejemplo de patrones de variación de proteínas estudiado por Hilu & Esen (1988) quienes evaluaron el potencial de estas proteínas (específica de los pastos) almacenadas en las semillas, como carácter macromolecular en la sistemática de este grupo de plantas. Los mencionados autores extrajeron prolamina de 33 especies representantes de seis subfamilias y los resultados les permitieron segregar las seis subfamilias en tres grupos, de acuerdo al tamaño de prolamina: 1) Pooideae,

2) Chlor-Panic-Arundinoideae, y 3) Orizo-Bambusoideae. Encontraron diversidad de prolamina en las Pooideae, subrayaron el nivel tribal de Bromaeae, sugirieron un posible linaje compartido para las Panicoideae y Chloridoideae así como también para las Bambusoideae y las Orizoideae. Por último sugirieron la cercanía entre Stipeae (una tribu polémica) y las Orizoideae y las Bambusoideae.

Los perfiles de aminoácidos de las proteínas es otra técnica poco empleada y de valor limitado en la sistemática de pastos, como se puede ver en el trabajo de Yeoh & Watson (1987).

Los estudios de la Alozimas, Isoenzimas, y del Acido Desoxirribonucleico (ADN) han empezado a producir resultados muy recientemente (en la última década) y se están perfeccionando actualmente. Los costos de los análisis moleculares para generar este tipo de información son muy altos, lo que limita la productividad en este rubro. De las casi 10,000 especies de gramíneas en el mundo, los estudios moleculares se han concentrado prácticamente en seis (las especies cultivadas de) *Avena*, *Hordeum*, *Triticum*, *Zea*, *Secale*, y *Oryza*. Más y más estudios de este tipo se están llevando a cabo en la actualidad y no está lejano el día en que se logre acumular información representativa de las subfamilias de Poaceae, lo que permitirá hacer nuevas conjeturas (o apoyar las existentes) de las relaciones evolutivas y posible origen de las gramíneas. Los fundamentos de estas técnicas moleculares pueden encontrarse en los trabajos de Gottlieb (1977) y Giannasi & Crawford (1986).

Un ejemplo de la aplicación de estudios alozímicos en biosistemática de pastos es el que se presenta a continuación. La variación genética cuantificada en el análisis de alozimas de las cuatro especies del género *Chaboissaea* se llevó a cabo recientemente por Herrera & Peterson (1994), permitió corroborar el origen monofilético de las especies disyuntas incluidas en este género (tres especies del noroeste de México y una de las pampas Argentinas), las cuales se consideraban anteriormente como especies de *Muhlenbergia* y fueron transferidas a *Chaboissaea* por Peterson & Annable (1992) con base en estudios de cromosomas y anatomía foliar.

ANALISIS NUMERICO DE LA INFORMACION PARA PRODUCIR UN SISTEMA DE CLASIFICACION

A medida que se fué generando información de diversas fuentes para un mismo grupo de plantas, el análisis y procesamiento de los datos acumulados fue cobrando dimensiones de mayor complicación. En la segunda mitad del presente siglo se desarrollaron varios métodos de análisis numérico de la información, que se basan en el principio de agrupación por similitudes. Sneath & Sokal (1973) presentan los fundamentos del análisis numérico con fines sistemáticos. Así, la clasificación fenética se inicia con el análisis numérico de

grandes cantidades de caracteres. El criterio principal para un análisis fenético es el grado de similitud y diferencia de todos los caracteres por igual, lo que produce un agrupamiento en forma de árbol llamado dendrograma. Los dendrogramas reflejan el grado de similitud entre un grupo de especies.

Ha partir de los descumbrimientos en genética y evolución se establecieron los fundamentos para la clasificaciones filogenéticas, en las que se busca que los miembros de un grupo taxonómico deben estar relacionados en forma más cercana entre si, que con aquellos miembros de otros grupos. Cuando se generalizó el uso del análisis fenético se pensó que el resultado práctico sería una clasificación filogenética, sin embargo se encontró que dos grupos diferentes pueden presentar características en común debido a una adaptación a condiciones similares, y no a que provengan de un ancestro común. Hennig (1966) fundamenta la escuela de pensamiento filogenético y establece que una clasificación filogenética debe permitir reconstruir la historia evolutiva de los taxa. En este tipo de clasificación algunos caracteres tienen mayor peso que otros, en base a los cambios evolutivos más importantes del grupo en estudio. El análisis numérico de dichos caracteres genera árboles de similitud evolutiva llamados cladogramas.

El valor de una clasificación depende del propósito con el que se lleve a cabo. Resolver problemas de relaciones filogenéticas puede ser el principal objetivo de los biosistemáticos y genetistas, no siendo así para aquellos que tienen necesidad de una clasificación taxonómica en terminos de nomenclatura, quienes seguramente preferirán los taxa reconocidos morfológicamente. Es importante subrayar que el favorecer las clasificaciones filogenéticas no significa que se ignore las determinaciones morfológicas de los taxa, sin embargo como menciona Barkworth (1992), un sistema de nomenclatura es realmente de valor si acepta los cambios que resulten de las inferencias filogenéticas, especialmente cuando éstas afecten la nomenclatura de los taxa.

La búsqueda no ha terminado; los biosistemáticos siguen tratando de proporcionar a los usuarios un sistema apropiado, perdurable y estable que se fundamente en una realidad biológica, a través de la cual los taxa puedan ser fácilmente reconocidos (Estes & Tyrl 1987).

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NEW SPECIES OF *NIEBLA* (RAMALINACEAE) FROM WESTERN NORTH AMERICA

P.A. Bowler & R.E. Riefner, Jr.

Department of Ecology and Evolutionary Biology; Museum of Systematic Biology, University of California, Irvine, California 92717 U.S.A.

P.W. Rundel

Environmental Biology Division, Laboratory of Biomedical and Environmental Sciences, University of California, Los Angeles, Los Angeles, California 90024 U.S.A.

J. Marsh & T.H. Nash, III

Department of Botany, Arizona State University, Tempe, Arizona 85287-1601 U.S.A.

ABSTRACT

Five new species of *Niebla* (Ramalinaceae) are described and a key to the North American taxa is presented. New species include *Niebla ceruchoides* Rundel & Bowler, *Niebla isidiaescens* Bowler, Marsh, Nash, & Riefner, *Niebla laevigata* Bowler & Rundel, *Niebla polymorpha* Bowler, Marsh, Nash, & Riefner, and *Niebla procera* Rundel & Bowler. Geographic ranges, habitat, and ecological notes are given for the five new taxa.

KEY WORDS: *Niebla ceruchoides*, *Niebla isidiaescens*, *Niebla laevigata*, *Niebla polymorpha*, *Niebla procera*, western North America, California, Baja California

INTRODUCTION

The genus *Niebla* occurs in western North America along the coast from Washington to Baja California Sur, México, as well as on the Channel Islands and islands adjacent to Baja California, and includes saxicolous, terricolous, and corticolous taxa (Rundel & Bowler 1977; Rundel, Bowler, & Mulroy 1972). The taxonomy of the group has not been well understood, and the lack of a key to the North American species has hampered consistent identification. The North American taxa all have black-chambered pycnidia and most species are aligned with either a homalioid lineage characterized by distinctive chondroid strands in the medulla or a ceruchoid affinity with a fluffy medulla lacking well formed chondroid strands. This study is part of a series on the genus, and describes five new species, as well as providing a key to the described taxa.

Most North American *Niebla* taxa can be arranged into two broad groups: (1) the "ceruchoid" group (with *N. ceruchis* [Ach.] Rundel & Bowler as a typical member) with a terpenoid chemistry and lacking in well developed chondroid strands, and (2) the "homalea" group (with *N. homalea* [Ach.] Rundel & Bowler as a typical member) with a more diverse chemistry including divaricatic, sekikaic, barbatic, protocetraric, or salazinic acids, and having conspicuous strands of chondroid material in the medulla. The *Niebla homalea* group includes the saxicolous *N. homalea* (divaricatic, barbatic, or sekikaic acids) and *N. josecuervoi* (Rundel & Bowler) Rundel & Bowler (salazinic acid), as well as their ground dwelling, bushlike morphologies, and the terricolous *N. pulchri-barbara* (Rundel & Bowler) Rundel & Bowler (protocetraric acid). *N. isidi-aescens* Bowler, Marsh, Nash, & Riefner is the isidiate derivative of *N. homalea*. It is saxicolous and is easily separated by the conspicuous coralloid isidia extending the length of the blades. The ceruchoid group includes the corticolous and polymorphic *N. ceruchis* and the sorediate *N. cephalota* (Tuck.) Rundel & Bowler. Saxicolous species include a group which are primarily cylindrical in cross-section and another species, *N. laevigata*, with a strongly flattened blade superficially resembling compressed morphologies of *N. homalea*, although *N. laevigata* has a terpenoid chemistry and lacks medullary chondroid strands. Saxicolous taxa in this group include *N. combeoides* (Nyl.) Rundel & Bowler, the longer, subpendulous *N. procera* Rundel & Bowler, and the short, inflated *N. robusta* (R.H. Howe) Rundel & Bowler. *Niebla cedroensis* is a recently described species (Marsh & Nash 1994) which is endemic to Cedros Island and the adjacent coast of Baja California. It is a plant which is easily separated due to its characteristically pale color and the large size it achieves. *Niebla polymorpha* is a saxicolous species with a broad ecological range, allowing it to occur further inland than any of the other ceruchoid chemistry taxa. The ceruchoid lineage taxa contain (-)-16 α -hydroxykaurane, with variable occurrences of zeorin, bourgeanic acid, and less frequently salazinic acid. A tuberculate species *in ed.*, endemic to the Morro Bay area in California, is remarkable in

the group by having a single chondroid strand in the medulla and terpenoid chemistry.

Key to the North American Species

1. Thallus sorediate. *N. cephalota*
1. Thallus esorediate. 2
 2. Corticolous. *N. ceruchis*
 2. Saxicolous or terricolous. 3
3. Thallus blades flattened with angular edges. 4
3. Thallus blades cylindrical (not flattened) without distinct edges. 9
 4. Within the medulla individual chondroid strands evident in cross section of blades. 5
 4. Within the medulla individual chondroid strands absent (but agglutinated hyphae forming a central cylinder may be present). 8
5. Medulla P+ red; California to Baja California. 6
5. Medulla P-; Baja California only. 7
 6. Medulla K+ yellow turning dark red (salazinic acid present); primarily saxicolous. *N. josecuervoii*
 6. Medulla K- (protocetraric acid present); terricolous. *N. pulchribarbara*
7. Thallus isidiate. *N. isidiaescens*
7. Thallus not isidiate. *N. homalea*
 8. Branches strap-like, strongly flattened in cross section; cortex typically smooth, plane. *N. laevigata*
 8. Branches not strap-like, irregularly prismatic in cross section; cortex typically rough, irregularly ridged. *N. polymorpha*
9. Mature thallus caespitose; blades short (3 cm). 10
9. Mature thallus becoming subpendulose; blades long (to 8 cm). 13
 10. Thallus spongy (compressible); branch tips blunt. *N. robusta*
 10. Thallus not spongy (solid); branch tips pointed. 11

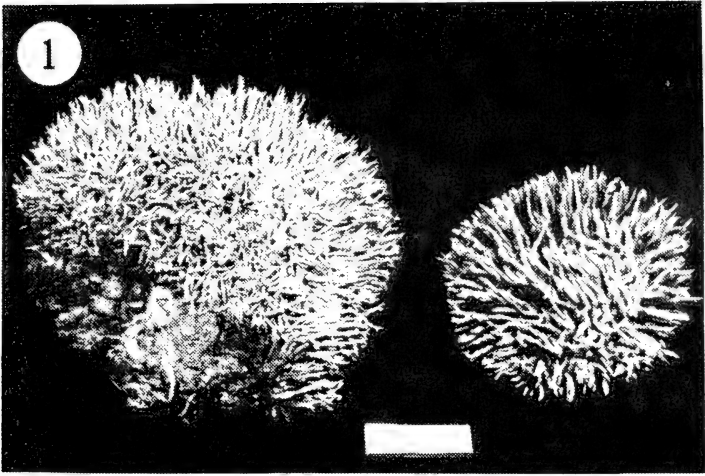
11. Secondary branching absent; apothecia terminal. *N. combeoides*
11. Secondary branching present, initiated basally; apothecia subterminal to terminal. 12
 12. Thallus isidiose-papillate, not forming dense cushions; branch tips rarely bifurcate; endemic of Morro Bay, California.
 *N. sp. nov. (in ed.)*
 12. Thallus not isidiose-papillate, forming dense cushions; branch tips typically bifurcate; occurring in both California and Baja California. *N. ceruchoides*
13. Cortex shiny, often maculate, yellow green; widely distributed in California and Baja California. *N. procera*
13. Cortex dull, not maculate, light yellow, becoming whitened frequently; an endemic of Cedros Island and the adjacent mainland. *N. cedroensis*

Taxonomy of the New North American *Niebla* Species

Niebla ceruchoides Rundel et Bowler, *sp. nov.* (Figure 1). *Ramalina ceruchoides* Magn. in Bendz, Sant., & Wachtm., Acta Chem. Scand. 9:1185. 1965. (*nomen nudum*). *Desmazieria ceruchoides* (Magn.) Follm. & Hun., Willdenowia 5:208. 1968. (*nomen nudum*). *Niebla ceruchoides* Rund. & Bowler, in ed., in Riefner, Phytologia 67(3):255. 1989. (*nomen nudum*). TYPE: U.S.A. California. Ventura Co.: On exposed outcrops along W. Portrero Road near Lewis Road, ca. 5 km from the ocean, *Riefner 89-388* (ASU); Isotypes: IRVC, COLO, WIS.

Thallus saxicolus vel irregulariter terricolus, fruticosus, erectus, cladinaformus, caespitosus, usque ad 6 cm altus. Rami cylindricus, <1.0(-1.5) mm lati, staminei, dense et intricate ramosus, apicem divaricatus. Cortex rigidus, medulla alba. Apothecia concavus, usque ad 7 mm diam., alba, rara, subterminalis vel terminalis. Sporidia 3-4 × 10-13 μm, uniseptatus. Pycnidia nigra. Acidum (-)-16α-hydroxykaurane, ± bourgeanicum, zeorin, usnicum, vel triterpeneus ignotum continens.

Thallus usually saxicolous, occasionally terricolous, cladinaform, densely branched, bushlike, resembling a small cushion plant. Branches subcylindrical to cylindrical, usually less than 1.0(-1.5) mm in diameter, mats 2-3 cm tall



Figures 1-2. Figure 1 (above). The type specimen of *Niebla ceruchoides*, Riefner 89-388 (ASU). Figure 2 (below). A representative specimen (left) of *Niebla isidiaescens*, Riefner 92-61 (IRVC) and a representative specimen (right) of *Niebla polymorpha*, Riefner 87-61a (IRVC). Bar = 1 cm.

(to 6 cm). Densely branching, branch tips divaricate as in some *Cladina* morphologies; color yellow-green becoming stramineous with age (sometimes pale gray-green in the field), cushion texture spiny. Branches more or less cylindrical, smooth or weakly fasciated. Cortex rigid when dry, cracking when bent. Medulla white, dense. Apothecial discs concave, to 7 mm, pale, uncommon, subterminal, but near the branch tips. Spores $3-4 \times 10-13 \mu\text{m}$. Black pycnidia borne on the attenuate branch tips, otherwise rare. Pycnospores straight, $3 \times 1 \mu\text{m}$.

Chemistry: (-)-16 α -hydroxykaurane, \pm bourgeanic acid, zeorin, unidentified triterpenes, usnic acid.

Distribution: This species occurs in widely isolated localities from Mt. Tamalpais, Marin County, California into northwestern Baja California and Guadalupe Island. It is abundant on the Channel Islands along the California coast, and also on Cedros Island off the northwestern coast of Baja California, México.

Habitat: This species occurs in widely isolated patches on coastal rocks, cliff faces, or less commonly on soil in sites with extensive exposure to wind and fog.

Representative Specimens Examined: MEXICO. Baja California: Punta Banda, *Bowler 20* (Herb. Rundel), *Bowler & Rundel s.n.*, November, 1972 (Herb. Rundel), *Bowler s.n.*, November, 1970 (Herb. Rundel); Guadalupe Island, *Weber & McCoy L-36641* (COLO); Sonorobampa Canyon, *Mulroy s.n.*, June, 1974 (Herb. Rundel); 40 km S of San Quintín and N of El Rosario, *Marsh 5970* (ASU); San Quintín, *Marsh 6950* (ASU); $31^{\circ}33'30''\text{N}$, $116^{\circ}42'\text{W}$, *Nash 25,196* (ASU); Cedros Island, north end, *Marsh 7292* (ASU); *Marsh 7269* (ASU); *Marsh 7397* (ASU); *Marsh 7338* (ASU).

U.S.A. California: Los Angeles Co.: Santa Catalina Island, *Weber & Santesson L-42800* (UC, Herb. Rundel); *Santesson 17903a*, *17909b* (UPS); Empire Landing area (Rippers Cove), *Marsh 6599* (ASU); Hamilton Beach NW of Avalon, *Marsh 6659* (ASU); Lands End on western end of Island, sub-isidiate, *Marsh 6612* (ASU); Lands End, *Marsh 6602* (ASU), *Marsh 6605* (ASU). San Clemente Island, *Santesson 17946*, *17977*, *18098* (UPS). Marin Co.: Mt. Tamalpais, *Riefner 85-717* (IRVC). Orange Co.: San Joaquin Hills, *Rundel s.n.* (Herb. Rundel); Aliso Canyon, *Gittens 8965* (Herb. Rundel), *Rundel s.n.* (Herb. Rundel), *Bowler s.n.*, 29 March 1987 (Herb. Bratt). Santa Barbara Co.: Santa Cruz Island, *Schuster 97b* (COLO), *Bratt 2907* (Herb. Bratt); Santa Rosa Island, *Nash 99,109* (ASU); South Point, *Marsh 6916* (ASU); lower portion of Cañada Lobos, *Marsh 6878* (ASU); lower end of Old Ranch Canyon, fertile, *Marsh 6818* (ASU); Santa Barbara Island, *Bratt 4827*, *3720*, *3695* (Herb. Bratt). San Luis Obispo Co.: Beach N of Hearst Castle, *Denison 30793* (OSU). Ventura Co.: 6 km N of Newbury Park, *Weber S1727*, *S1727A* (COLO,UPS); E of Camarillo State Hospital, *Malachowski 1* (Herb. Rundel); W Portrero Rd. 5 km from ocean, *Riefner 89-388* (ASU,IRVC,COLO,WIS).

Sorediate form: U.S.A. California: Santa Barbara Co.: Santa Barbara Island, Bratt 4813, 3660, 4872, 5171, 3722, 3707 (Herb. Bratt).

Niebla ceruchoides resembles a cushion plant or bryophyte in habit, and is cladinaform in appearance, particularly accentuated by the dense mat-like form it takes and the bifurcate branch tips occurring in some Cladinae. The cushion-like growth form with thin branches and a compact mat of branch tips makes it well adapted to fragmentation and vegetative reproduction. It is usually sterile. Most cladinaform lichens are fistulose, however, *N. ceruchoides* has solid, medulla-filled branches even though it superficially resembles a *Cladina* in growth form and branching. Its spiked, bushlike form makes it resemble a miniature hedge-hog, and it is a compact fog and moisture trap.

This species description formally establishes a taxon known until now by the nomen nudum *Desmazieria ceruchoides*. The name *Ramalina ceruchoides* was first used by Santesson in field notes from Chile (R. Santesson, personal communication). This name was subsequently cited by Bendz, et al. (1965) in a study of the species' chemistry, with the notation that it was not yet a formally described taxon. The new and invalid combination *Desmazieria ceruchoides* was made by Follmann & Huneck (1968) in the erroneous belief that the species was validly published. Neither Magnusson nor anyone else did in fact describe the taxon.

Niebla ceruchoides is a species which requires fog, is nearly invariably found in northwest facing exposures, and often lies at the lower level of the *Niebla* zone. It frequently occurs at the lip of a cliff or on rocks situated to receive direct exposure to onshore fog bearing breezes as much as 8 km inland, such as the western Santa Monica Mountains, Ventura County. Its occurrence on soil is an expression of its tolerance within its microhabitat, as it occurs abundantly on several substrates in these habitats; its preferred habitat is rock or loess soils, but it can exist on adjacent rocky soils. This species' growth form makes it a well adapted strainer for airborne moisture, and it also serves as a seed and germination trap for some cliff dwelling vascular plants such as *Dudleya* spp. (Riefner & Bowler 1994).

This species occurs in valleys along coastal southern California and northwestern Baja California. In these habitats it is extremely abundant at some localities, for example, on Santa Rosa Island.

Niebla isidiaescens Bowler, Marsh, Nash, et Riefner, *sp. nov.* (Figure 2).

TYPE: MEXICO. Baja California Sur: 3.5 km along road to Punta Abrejos from Highway 1, on a hill at 120 m, Marsh 6142 (ASU).

Thallus saxicolus, caespitosus, similis ad *Niebla homalea* (Ach.) Rundel & Bowler, rami straminea vel flavo-virentes, applanati vel subcylindricus, vel 1.2 cm lati, 3.5 cm longus, isidia marginalia

et laminalia. Cortex rigidus, medulla ad strandus. Apothecia rara, subterminalis, discus usque ad 7 mm. Sporae $10-14 \times 3-4 \mu\text{m}$. Pycnidia negra. Acidum sekikaicum vel divaricatum, usnicum, triterpenes continens.

Thallus saxicolous, fruticose, shrublike, flattened or subcylindrical branches similar to *Niebla homalea* in variability, to 1.2 cm in breadth (usually less than 0.5 cm) and 3.5 cm in length, branching laterally from straplike blades or unbranched from smaller cushion-like tufted thalli; color yellow-green. Branches solid, flattened or subcylindrical, smooth, with abundant coralloid isidia extending the length of the branches on both the blade surfaces and on the blade edges with varying degrees of density. Isidia tips blunt. Cortex rigid, similar in anatomy to *N. homalea* consistently with chondroid strands embedded in the white medulla. Apothecia rare, disc up to 7 mm diameter. Spores unisepate, $10-14 \times 3-4 \mu\text{m}$, usually straight, rarely gently curved. Pycnidia black, uncommon on some plants, common on others. Pycnospores straight, $4.5-6.0 \times 1.5 \mu\text{m}$.

Chemistry: Sekikaic or divaricatic acids, usnic acid, triterpenes.

Distribution: The Channel Islands off California, Santa Monica Mountains, Ventura County on the mainland, and northwestern Baja California from San Quintín south to central Baja California Sur, and Cedros Island.

Habitat: This is a saxicolous species occurring on outcrops and rocks in open maritime scrub habitats.

Representative Specimens Examined: *Divaricatic acid race*: MEXICO. Baja California: San Quintín, Cerro Kenton, *Marsh 6926, 6925* (ASU). Baja California Sur: 3.5 km along road to Punta Abreojos from Hwy 1, fertile, *Marsh 6190, 6128, 6199, 6155* (ASU); 152 km on road turnoff 2.4 km to Puerto Nuevo, Vizcaino Peninsula, *Marsh 4258, 4262a, 4261, 4263* (ASU); 1.6 km E of Bahía Tortuga, *Marsh 4277a* (ASU); 31 km W of San Ignacio, *Nash 26, 147* (ASU); 31 km W of San Ignacio, *Marsh 4994a* (ASU).

U.S.A. California: Los Angeles Co.: Santa Catalina Island, Lands End, *Marsh 6611, 6618, 6614* (ASU); ridge above Blue Cavern Point, *Marsh 6625, 6628, 6633* (ASU).

Sekikaic acid race: MEXICO. Baja California Sur: 31 km W of San Ignacio, *Marsh 4901, 4995* (ASU).

U.S.A. California: Los Angeles Co.: Santa Catalina Island, Lands End, *Marsh 6604* (ASU). Ventura Co.: Conejo Mountain, *Riefner 92-61* (IRVC).

Additional specimens (chemistry not examined): MEXICO. Baja California: Cedros Island, north end, *Marsh 7293, 7296, 7299, 7300, 7348* (ASU).

Niebla isidiaescens is the isidiate species pair taxon of *N. homalea*. It is rarely fertile and is extremely variable in its morphology. The coralloid isidia are blunt and are easily broken away from cortex surfaces.

Niebla laevigata Bowler et Rundel, *sp. nov.* (Figure 3). TYPE: U.S.A. California: San Luis Obispo Co.: On exposed rock in fog stream zone of Coon Creek Canyon at Montana de Oro State Park, *Riefner 87-394* (ASU).

Thallus saxicolus, fruticosus, rami applanati, 2.5 cm lati, rigidus usque ad 5(-6) cm altus. Rami flavo-virentes, ramifacatio rara. Medulla alba, non strandus continens. Sporis 10-14 \times 4-5 μ m, uniseptatus. Acidum (-)-16 α -hydroxykaurane, zeorin, \pm bourgeanicum, usnicum continens.

Thallus saxicolous, fruticose. Branches strongly compressed and flattened, external cortex smooth and far less ridged than in the *Niebla homalea* group. Lacinae to 2.5 cm wide and 5(-6) cm long, commonly 1 cm broad and 2.5 cm in length, usually as straplike, flat, unbranched blades, though in aberrant forms it can be wider and less smooth. Branches arising as a tuft from a basal plate; color light yellow-green to green, usually blackened basally, texture smooth to gently ridged. Branches solid, cortex very rigid, friable, cracking when bent, usually smooth, occasionally reticulate ridged. Cortex a thick palisade formation overlying a thinner supportive layer, chondroid strands absent in the medulla. White deposits of crystalline (-)-16 α -hydroxykaurane present along cortical cracks. Medulla white, fluffy, and lacking the chondroid strands which are conspicuous in the *N. homalea* group. Apothecia common, primarily terminal, often clumped on the terminal margins of blade apices, disc concave, often curled inward and lobed, whitish, up to 8 mm in diameter but usually much smaller (4 mm). Spores 10-14 \times 4-5 μ m, straight to gently curved; rarely strongly curved. Black chambered pycnidia present, particularly on the terminal half of the blade, along the margins and on any ridges which occur. Pycnospores straight, 4.0-5.5 \times 1 μ m.

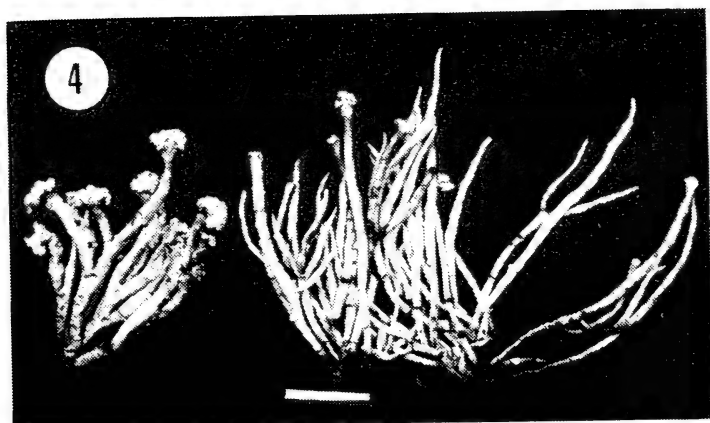
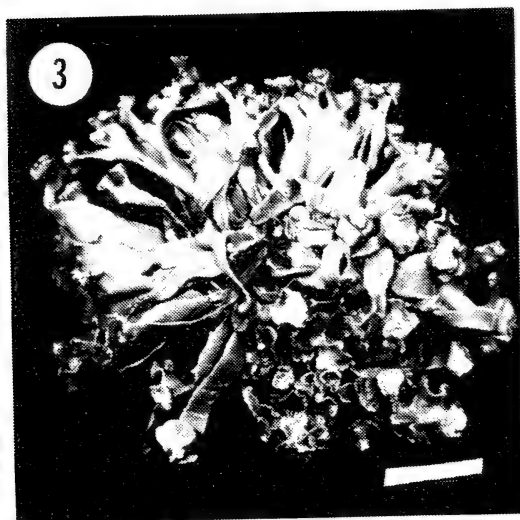
Chemistry: (-)-16 α -hydroxykaurane, zeorin, + bourgeanic acid, usnic acid.

Distribution: From San Francisco to northwestern and central Baja California, including Vizcaíno and Cedros Island.

Habitat: Saxicolous on boulders or cliff faces in sites well exposed to coastal onshore wind and fog.

Representative Specimens Examined: MEXICO. Baja California: Punta Banda, *Bowler 28*; Los Arbolitos, *Bowler s.n.*, November, 1970 (Herb. Rundel); *Bowler s.n.*, 25 November 1970 (Herb. Rundel), *Nash 4907* (ASU); 6 mi S of Miller's Landing, *Nash 9006* (Herb. Rundel); San Quintín, thalli observed by P.A. Bowler.

U.S.A. California: Alameda Co.: Berkeley Campus, *Howe s.n.*, 1873 (UC). Los Angeles Co.: Santa Catalina Island, *Hasse 209* (FH), *Hasse s.n.*, 1906 (US), *Santesson 17904* (UPS), *Weber & Santesson L-42799* (COLO), *St. John*



Figures 3-4. Figure 3 (above). The type specimen of *Niebla laevigata*, Riefner 87-394 (ASU). Figure 4 (below). The type specimen of *Niebla procera*, Riefner 87-100 (ASU). Bar = 1 cm.

s.n., 22 August 1971 (Herb. Rundel). Marin Co.: Willow Camp, *Parks s.n.*, 1972 (H,UC). Monterey Co.: *Farlow s.n.*, 1885 (UC); Willow Creek, *Rundel 3730, 3732* (Herb. Rundel); Pt. Lobos State Reserve, *Bratt 3788* (Herb. Bratt). Santa Barbara Co.: Santa Barbara Island, *Bratt 3634, 4816, 3637, 5172, 3717, 4851, 4821* (Herb. Bratt); Santa Cruz Island, *Bratt 1599* (Herb. Bratt); San Nicolas Island, *Foreman L-44286* (COLO); Anacapa Island, middle island, *Goeblich s.n.*, 1963 (UC); Santa Rosa Island, East Point, *Marsh 6813* (ASU), N slope above Channel, *Marsh 6934* (ASU). San Diego Co.: San Diego, *Palmer s.n.*, 1888 (H).

Niebla laevigata superficially resembles *N. homalea*. It is both morphologically and chemically distinct, however. It can commonly be distinguished in its northern reaches by its unridged, smooth, shiny, bright yellow thallus, differing from the typically ridged, plated, angular, and dull cortex of *N. homalea*. In northwestern Baja California (Punta Banda), the species has a more ridged blade, but its lanceolate appearance makes it easily separable from *N. homalea*, from which *N. laevigata* is also ecologically separated in local microhabitats. For example, *N. homalea* occurs in a far broader range in elevation than *N. laevigata*, which is restricted to low elevation, ocean-facing saxicolous exposures. Thalli of *N. homalea* may have a bright yellow and shiny surface, but they still retain a plated surface. *Niebla laevigata* usually arises from a blackened base as discrete unbranching blades from a basal attachment point, while *N. homalea* usually branches and frequently has marginal proliferations, not present in *N. laevigata*.

Although it may be locally abundant, *Niebla laevigata* is known from widely scattered localities on the coast from central California and the Channel Islands to northwestern Baja California. It occurs with *N. homalea* in these localities, but its ecological habitat is typically distinct. This species is usually low in the supralittoral *Niebla* zone at about the same height and exposure as *N. robusta*. Rarely *N. laevigata* occurs inland where low inversion fogs funnel through canyons and valleys.

Niebla laevigata is anatomically very similar to *N. homalea*, although it possesses a terpenoid chemistry indicating a ceruchoid lineage (Bowler 1981). *Niebla robusta* has a much thicker supportive tissue. Both *N. laevigata* and *N. robusta* lack large chondroid strands in the medulla, while all saxicolous chemomorphs of *N. homalea* have them.

Niebla laevigata occurs in scattered localities on coastal bluffs in California, the California Channel Islands, and along coastal northwestern and central Baja California, and on islands such as Cedros Island along the coast of Baja California.

Niebla polymorpha Bowler, Marsh, Nash, et Riefner, *sp. nov.* (Figure 2). TYPE: U.S.A. California: Los Angeles Co.: Santa Catalina Island,

Marsh 6206 (ASU).

Thallus saxicolus, caespitosus, rara ramosus. Rami irregulariter compressi vel applanati, usque ad 6 mm lati. Cortex rigidus, flavo-virentes, medulla alba sans strandus. Apothecia terminalus, frequentia ad triplets, disc usque ad 5 mm diam. Sporis (10-) 12-14(-15) \times 3.0-3.5(-4.0) μ m. Acidum bourgeanicum, (-)-16 α -hydroxykaurane, zeorin, \pm salazinicum, usnicum continens.

Thallus saxicolous, clumped and tufted, branching relatively sparse. Branches irregularly compressed sometimes flattened to 6 mm in width, the surface crinkled and irregularly lacunose. Cortex greenish-yellow. Medulla white, without well developed embedded chondroid strands. Apothecia primarily terminal, often in triplets. Disc cupped and pale greenish-white, to ca. 5 mm in diameter. Spores uniseptate, (10-)12-14(-15) \times 3.0-3.5(-4.0) μ m, straight or slightly curved. Pycnidia black, primarily situated along the ridged areas of the blades. Pycnospores straight, 4-5 \times 1.5 μ m.

Chemistry: Bourgeanic acid, (-)-16 α -hydroxykaurane, zeorin, \pm salazinic acid, usnic acid.

Distribution: Ventura County, California south into northwestern Baja California, México.

Habitat: *Niebla polymorpha* is saxicolous, occurring on boulders and cliffs. It is often the most inland and xeric species of this coastally influenced or associated genus group.

Representative specimens examined: U.S.A. California: Los Angeles Co.: Santa Catalina Island, Above Fisherman's Cove, *Marsh 6502* (ASU), Lands End, *Marsh 6606* (ASU). Orange Co.: Aliso Canyon, *Gittins 8966* (Herb. Rundel), Aliso Creek, *Riefner 87-61a* (IRVC). Ventura Co.: Conejo Mtn., *Riefner 92-80*.

Niebla polymorpha most closely resembles a deformed *N. robusta* which has smaller spores of 10-12 μ m, inflated, rounded branches, and larger urn-shaped apothecia. *Niebla polymorpha* occupies the more xeric zones inland from the immediate coast and is associated with divaricatic acid and barbatic acid populations of *N. homalea*.

***Niebla procera* Rundel et Bowler, sp. nov.** (Figure 4). TYPE: U.S.A. California: San Luis Obispo Co.: Found on rock outcrops in high marsh at Morro Bay State Park, *Riefner 87-100* (ASU).

Thallus saxicolus, fruticosus, subpendulosus. Rami straminei, cylindricus vel subcylindricus, 1-2(-4) mm lati, usque ad 8 cm altus. Cortex rigidus, medulla alba. Apothecia terminalus vel subterminalus, disc concavus vel convexus, usque ad 6 mm diam.

Sporis rectis, 11.0-12.5(-13.0) \times 3.5(-4.0) μ m. Pycnidia negra. Acidum (-)-16 α -hydroxykaurane, \pm zeorin, \pm salazinicum, terpenes, \pm usnicum continens.

Thallus saxicolous, fruticose, subpendulous in large plants. Branches cylindrical or sub-cylindrical (slightly angular), 1-2(-4) mm in diameter, to ca. 8 cm in length, sparingly branching, occasionally with short lateral branchlet proliferation, the branchlets from the major branches often perpendicular to the branch axis. Branch apices pointed. Color greenish-yellow, with black spots of necrotic tissue, branches often blackened on one side. Branches solid and stiff, unridged and without the angular plates found in the *Niebla homalea* group. Cortex rigid, friable and smooth, and cracking when bent, similar to *N. robusta*. Apothecia common, terminal or subterminal, either single or clustered. Disc concave to convex and frequently lobed, whitish to tan, up to 6 mm in diameter. Thallus usually blackened around the base. Medulla white, lacking chondroid strands. Spores straight, 11.0-12.5(-13.0) \times 3.5(-4.0) μ m. Black-chambered pycnidia present, but less numerous than in many other *Niebla* species. White fluffy deposits of (-)-16 α -hydroxykaurane are present in most herbarium specimens. Black-chambered pycnidia laminal and subterminal, but not as abundant as in many other *Nieblae*. Pycnosporos straight, 4.0 \times 1.5 μ m.

Chemistry: (-)-16 α -hydroxykaurane, \pm zeorin, \pm salazinic acid, terpenes, fatty acids, \pm usnic acid.

Distribution: Coastal Baja California, Cedros Island, Guadalupe Island, coastal south and central California, and the Channel Islands.

Habitat: Coastal rocks and cliffs along the immediate seashore.

Representative Specimens Examined: MEXICO. Baja California: Guadalupe Island, *Palmer s.n.*, 1889 (US); *Weber & McCoy L-36505* (COLO); Colina del Suroeste at San Quintín Bay, *Bowler s.n.*, 28 March 1971 (Herb. Rundel); San Quintín, *Marsh 6341, 6349, 6348, 6350a, 6307, 6346* (ASU); Cedros Island, north end, *Marsh 7266, 7255* (ASU). Baja California Sur: 3.5 km along road to Punta Abreojos from Hwy 1, hill 60-260 m, *Marsh 6193, 6191, 6140, 6155* (ASU).

U.S.A. California: Los Angeles Co.: San Miguel Point, *Grigarick & Schuster L-53661* (CANL); Santa Catalina Island, Lands End, *Marsh 6624* (ASU). Monterey Co.: *Weber 8245* (COLO), *Weber 8245A* (DUKE); Willow Creek, *Rundel s.n.* (Herb. Rundel); No locality, *Eisen s.n.*, 1874 (US). Santa Barbara Co.: San Miguel Island, *DeSmith 1319* (Herb. Bratt); Santa Rosa Island, lower portion of Cañada Lobos, *Marsh 6880, 6879* (ASU); pass along the main road just SE of Black Mountain, *Marsh 6716* (ASU); South Point, *Marsh 6915* (ASU); Santa Cruz Island, bluff top south of Forney Cove, *Bratt 5291* (Herb. Bratt, IRVC).

Niebla procera resembles the maculate form of *N. ceruchis*, but can be

distinguished by its much larger size, stiffer cylindrical branches, and its occurrence on saxicolous rather than corticolous substrates. It has a combeoid cortex (with *N. combeoides* as a typical member) and lacks thick medullary chondroid strands, as do nearly all of the ceruchoid lineage taxa. This characteristic species appears to be most closely related to *N. robusta*, and inhabits coastal rocks and cliffs which lie below the *N. homalea* zone and above the splash zone of the supralittoral sensu Ryan (1988). It occurs south along coastal northwestern Baja California to San Quintín, Cedros Island, and Punta Arbojos in Baja California Sur. This is a saxicolous species usually found near the ocean in exposures experiencing coastal fog.

ACKNOWLEDGMENTS

We are grateful to the Curators of the many herbaria consulted during this study, and of their kindness in providing numerous loans over the past twenty years. Primary herbaria and individual collections examined include the ASU, Bratt Herbarium, CANL, COLO, DUKE, FH, H, IRVC, LAM, MICH, MSC, OSU, PC, SBM, SF, UC, US, and UPS. The assistance of National Science Foundation grant BSR 9201111 is appreciatively acknowledged for making this collaboration possible. We thank Chicita Culberson and Anita Johnson for verifying the chemistry of a number of specimens, and David Williams for photography. We are particularly grateful to Roger Rosentreter and John W. Thomson for reviewing an early draft of the manuscript.

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REVISIONARY STUDY OF *LASIARRHENUM* (BORAGINACEAE)

Billie L. Turner

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

Lasiarrhenum, regarded by I.M. Johnston (1954) as monotypic, is treated as having three species: *L. trinervium* (Lehm.) B.L. Turner, *comb. nov.* [an earlier name for *L. strigosum* (H.B.K.) I.M. Johnst., the generitype]; *L. pinetorum* I.M. Johnst. (upon which Johnston erected the monotypic genus *Perittostema* I.M. Johnst.); and *L. confundum* B.L. Turner, *sp. nov.*, a localized endemic from southwestern Durango, México. Since the latter species possesses characters which bridge the "morphological gap" between *Lasiarrhenum* and *Perittostema*, I have reunited the two genera, much as Johnston originally treated these. Distributional maps, key to species, and complete synonymy are given for the taxa concerned.

KEY WORDS: Boraginaceae, *Lasiarrhenum*, *Perittostema*, México

The genus *Lasiarrhenum* was erected as monotypic by Johnston in 1924, and maintained by him in his subsequent account of the Mexican borages (Johnston 1954). Since he rendered an excellent description of the single species involved, such is not repeated here, but I have emended the generic description of *Lasiarrhenum* to include *L. pinetorum* (which Johnston described in 1935 but subsequently created for this the monotypic genus *Perittostema*) and *L. confundum*, described herein.

Johnston (1954) summarized his views on relationships among genera of the tribe Lithospermae for North America. In this, *Lasiarrhenum* and *Perittostema* were positioned near the genera *Lithospermum*, *Macromeria*, and *Onosmodium*. My taxonomic interest in the latter two genera prompted the present study.

LASIARRHENUM I.M. Johnst., emended.*Perittostema* I.M. Johnst.

The genus remains essentially as described in detail by Johnston (1954) except that the following emendations seem in order: corollas 10-25 mm long; stamens may have ligulate or short trianguliform filaments; anthers either pubescent or glabrous on their dorsal surfaces; thecae of anthers yellow or dark-colored with thick ovate to truncate appendages, the connectives with or without a terminal mucro.

Type species, *Lasiarrhenum trinervium* (Lehm.) B.L. Turner [= *L. strigosum* (H.B.K.) I.M. Johnst.].

KEY TO SPECIES

1. Anthers densely pubescent dorsally. 1. *L. trinervium*
1. Anthers glabrous dorsally. (2)
 2. Filaments ca. 1 mm long, trianguliform; corollas ca. 10 mm long. .
..... 2. *L. pinetorum*
 2. Filaments 3-4 mm long, ligulate; corollas ca. 20 mm long.
..... 3. *L. confundum*

1. **LASIARRHENUM TRINERVIUM** (Lehm.) B.L. Turner, *comb. nov.*
 BASIONYM: *Onosma trinervium* Lehm., *Asperif.* 2:37. 1818 (Sep-Oct).
 TYPE: MEXICO. "Habitat in America Meridionali", w/o collector,
 w/o date, but probably based upon Humboldt and Bonpland collections
 from Michoacán in 1803, noted below (type material is said by Stafleu
 & Cowan [1979] to probably reside at Melbourne, Australia, but D.B.
 Foreman [pers. comm.] at MEL could not verify this).

Onosma strigosum H.B.K., *Nov. Gen. & Sp.* 3:93. 1819 (8 Feb). *Onosmodium strigosum* (H.B.K.) Don, *Gen. Syst.* 4:317. 1837. *Lasiarrhenum strigosum* (H.B.K.) I.M. Johnst., *Contr. Gray Herb.* 70:15. 1924. TYPE: MEXICO. Michoacán: vicinity of Patzcuaro, Sep 1803, *Humboldt & Bonpland s.n.* (HOLOTYPE: P).

Lithospermum longifolium Willd. in Roem. & Schultes, *Syst.* 4:742. 1819. TYPE: MEXICO. probably based upon same type as *Onosma strigosum* H.B.K. (HOLOTYPE: P?; Probable isotype: F!).

Onosmodium eriocaulon A.DC., *Prodr.* 10:70. 1846. TYPE: MEXICO. Morelos (?): "Cordillera de Guchilaque", w/o date, J.L. Berlandier 1020 (HOLOTYPE: P; Holotype fragment: GH!; Phototypes: CAS-DS!, F!, MICH!).

Lasiarrhenum lundellii I.M. Johnst., *Wrightia* 2:15. 1959. TYPE: MEXICO. Oaxaca: Mpio. Tlacolula, mountain side in pine woodlands, above Tejocote, 25 Jul 1943, C.L. Lundell 12296 (HOLOTYPE: LL!; Isotype: MICH!). Consultation of Lundell's field notes (LL) reveals this locality to be near Mitla, Oaxaca, although I could not locate Tejocote on maps available to me.

Johnston (1954) gives a very fine descriptive account of this species, and such is not repeated here. Unfortunately he took up the name *Lasiarrhenum strigosum* in ignorance of the chronology. The earliest available name, *Onosma trinervium* Lehm., predates *O. strigosum* H.B.K. by several months, according to publication data presented by Stafleu & Cowan (1979).

Lasiarrhenum lundellii was said by Johnston to differ from *L. strigosum* [= *L. trinervium*] in having a lower habit with fewer-flowered racemes and obovoid corollas, the latter lacking a well defined throat and tube. He further notes that *L. lundellii* has a broadly obconic stigma which is obscurely bilobed. I find these to be highly variable characters throughout the range of *L. trinervium*. Type material of *L. lundellii* does appear to have a softer more uniform vestiture than occurs in most specimens of *L. trinervium*, but overall the specimens concerned seem only weakly differentiated from the latter and scarcely worth taxonomic recognition.

Lasiarrhenum trinervium is a widespread relatively homogeneous species notable for its broad, fleshy ligulate filaments, and markedly appendaged anthers which are abundantly white-hairy on the back. In habit and corolla shape it superficially resembles a species of *Onosmodium*, but Johnston thought its closest relationship to be with *Nomosa*, reasons for which he expounded upon in some detail. It should prove interesting to check his presumably phyletically oriented views with DNA data.

REPRESENTATIVE SPECIMENS: MEXICO. Hidalgo: *Rzedowski 33425* (CAS,MEXU); *West G-9* (WIS). Jalisco: *Anderson 5137* (MICH,NY); *Fuentes 605* (MO); *McVaugh 13049, 13523* (GH,MICH); *Palmer 173* (GM,MEXU, MO,NY,PH,US). México: *Hinton 1533* (GH,MO,NY); *Hinton 5064* (GH, NY,US); *Hinton 8274* (F,GH,LL,MO,NY); *Lundell 12647* (LL,MICH); *Mezía 2710* (CAS,MICH,MO,NY,PH,WIS). Michoacán: *Hinton 15435* (CAS-DS,F, GH,MICH,NY,US); *Leavenworth 545* (F,GH,NY); *Leavenworth 317* (F,MO); *Pringle 4131* (F,GH,MO,NY,US). Morelos: *Fearing 128* (TEX,US); *Hinton 17513* (F,MICH,MO,TEX); *Lyonnet 1848* (CAS,MEXU,US); *Pringle 9124* (F,GH,MEXU,MO,US). Nayarit: *Pennell 19980* (GH,MICH,NY). Oaxaca:

Ghiesbreght s.n. (GH); *Orcutt s.n.* (MO). Puebla: *Roe 345* (NY,WIS); *Weaver 983* (GH,US). Veracruz: *Nevling 1974* (F,MEXU,NY).

The two collections cited from Oaxaca are fairly typical in appearance, in spite of their relative isolation from the main body of collections.

2. *LASIARRHENUM PINETORUM* I.M. Johnst., J. Arnold Arb. 16:187. 1935. *Perittostema pinetorum* (I.M. Johnst.) I.M. Johnst., J. Arnold Arb. 35:30. 1954. TYPE: MEXICO. Oaxaca: w/o specific locality, Sep 1841(?), *Ghiesbreght 311* (HOLOTYPE: P).

I have not examined material of this taxon. As noted by Johnston (1954), the species is known only by a single specimen with only two mature corollas. Nevertheless, he provided a very detailed thorough description and this need not be repeated here. I have guessed that its type locality (Figure 1) might be near Yavesia, Oaxaca, where Ghiesbreght was known to have collected in the period concerned.

3. *LASIARRHENUM CONFUNDUM* B.L. Turner, *sp. nov.* TYPE: MEXICO. Durango: Mpio. de El Salto, SE face of El Espinozo del Diablo, 20 km SE of La Ciudad, 2770 m, 12 Sep 1979, *D.E. Breedlove 43946* (HOLOTYPE: CAS!).

Lasiarrheno pinetoro I.M. Johnston similis sed staminibus filamentis ligulatis (vs. filamentis triangularibus), corollis longioribus (ca. 20 mm longis vs. 10 mm), et foliis ellipticis plerumque 20-35 mm latisque (vs. lineari-subulatis 1-2 mm latisque) differt.

Erect perennial herbs 35-65 cm high. Stems pubescent with pilose appressed or spreading hairs 1-3 mm long. Midstem leaves elliptical to elliptic-oblong, sessile, 6-8 cm long, 2.0-3.5 cm wide, sparsely pubescent with both minute strigose and appressed long-pilose hairs, pinnately nervate in the manner of *Cornus*. Flowers arranged in 1-3 terminal bracteate secund racemes 3-15 cm long (from first anthesis into late fruiting stages), the pedicels ca. 2 mm long in flower, in fruit 3-11 mm long. Calyces 7-9 mm long, the lobes linear-lanceolate, ca. 1 mm wide. Corollas "white with greenish tip", ca. 20 mm long, appressed pilose without, glabrous within, except for a very sparse array of minute glandular hairs in the area where faucal appendages usually occur, although the latter scarcely obvious in the present species; lobes broadly rounded, 2.5-3.0 mm wide, ca. 1.5 mm long, glabrous within, strigose without. Stamens about equally attached 7-8 mm below the base of the lobes; filaments ligulate, glabrous, 3-4 mm long, 0.8-1.0 mm wide, attached 1-2 mm below midpoint of the connective at ca. 1/3 the staminal length; anthers ca.

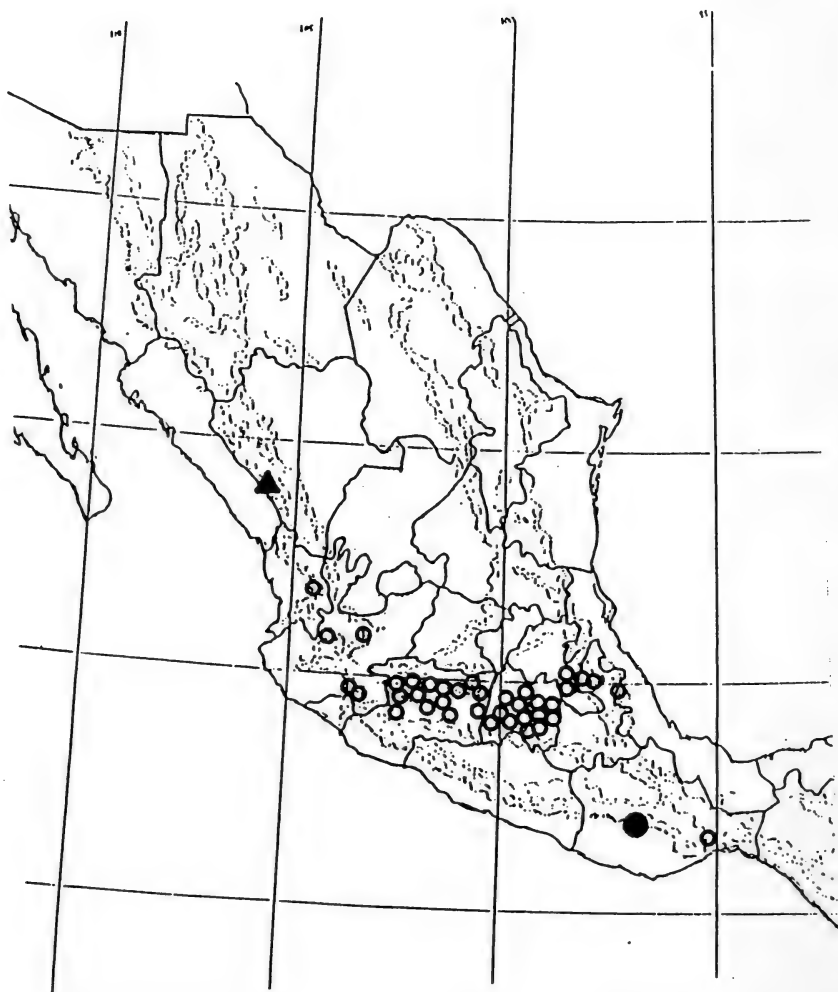


Figure 1. Distribution of *Lasiarrhenum trinervium* (open circles), *L. pinetorum* (closed circle), and *L. confundum* (triangle).

3 mm long, the terminal appendage truncate, ca. 0.25 mm long, terminated by an abrupt mucro ca. 0.1 mm long, at maturity the thecae of lower portion of the anthers separating so as to give the anther a sagittate appearance, the anthers extending to or near the base of the corolla lobes but not exerted. Style glabrous, exerted for 3-10 mm beyond the corollas, the apices bifid, forming two flabellate stigmatic arms ca. 0.25 mm long, 0.4 mm wide. Nutlets off-white, glossy, ca. 3 mm long, 2 mm wide, with a weak ventral ridge.

As indicated by its name, this taxon has confounded my ability to position it as to genus. It superficially resembles a species of *Macromeria* or *Onosmodium* but has markedly different stamens from either of these. In Johnston's (1954) key to the genera of the Lithospermae, the species will begrudgingly key to *Perittostema* (assuming the "throat of corolla [to be] decorated with appendages, stipitate glands or abundant hairs"), but the faucal appendages are weakly developed, if at all, and the leaves have well-developed nerves. Johnston in his description of *Perittostema*, which is based upon a single sheet at P with only two flowers collected by *Ghiesbreght* somewhere in southern México, noted that "The filaments of *Perittostema* are unique [among the Lithospermae]." He went on to describe the very short firm trianguliform filaments in some detail, followed by an account of the anthers. While the filament description does not match that of the presently described species, most other characters appear reasonably close, except for the "dark-colored" thecae margins and recurved mucro. Johnston noted that "The only member of Lithospermae with filaments even suggestive of those of *Perittostema* is the genus *Lasiarrhenum*. In the latter genus the filaments are compressed and are broadened upward, but are much larger and more elongate, being oblanceolate rather than triangular." The presently described taxon has the filaments of *Lasiarrhenum* but the anthers of *Perittostema* (the dorsal surface of anthers of *Lasiarrhenum* being markedly pubescent throughout, including its well developed apical appendage, vs. glabrous in *Perittostema*). In short, *L. confundum* has the filaments of *Lasiarrhenum* but anthers of *Perittostema*, effectively vitiating any strong distinction between these two genera. Because of this I position *Perittostema pinetorum* in the genus *Lasiarrhenum*, as originally done by Johnston.

ACKNOWLEDGMENTS

I am grateful to Guy Nesom for the Latin diagnosis and to him and Alan Prather for reviewing the paper. My study is based largely upon material on loan from the following institutions: ARIZ, CAS, F, GH, KANU, LL, MEXU, MICH, MO, NY, OKLA, PH, TEX, UC, US, WIS. This material, totaling 100 or more sheets has been annotated and serves as a basis for the distributional maps depicted in Figure 1.

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REVISIONARY STUDY OF THE GENUS *ALLIONIA* (NYCTAGINACEAE)

B.L. Turner

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

Allionia is a genus with two widespread partially sympatric species, *A. choisyi* and *A. incarnata*. Both occur throughout the warmer more xeric regions of North and South America and are abundantly represented in herbaria. *Allionia choisyi* does not appear to have meaningful morphogeographical infraspecific categories in either North or South America. *Allionia incarnata*, however, appears to have three well-marked but intergrading morphogeographical infraspecific taxa in North America: var. *incarnata*, a widespread weedy taxon primarily centered in North America but extending into South America; var. *nudata* (Standl.) Munz, largely confined to the Sonoran desert regions of México and closely adjacent U.S.A. (southern California, southern Nevada, and southwestern Arizona); and var. *villosa* (Standl.) B.L. Turner, *comb. nov.*, largely confined to the intermontane region of Nevada and Utah southwards to northern México. Keys to the taxa are provided along with maps showing their distribution.

KEY WORDS: Nyctaginaceae, *Allionia*, taxonomy

Allionia, as treated here, is a genus of only two widespread sympatric species, one for which (*A. incarnata*) various infraspecific categories have been proposed. The genus has had a checkered nomenclatural history, some of the early workers (e.g., Standley 1918) incorrectly took up the generic name *Wedelia* Loebl. (not *Wedelia* Jacq.) for its members, but its correct name is *Allionia* L., first proposed by Linnaeus in 1759 and typified by material of *Allionia incarnata* from the coastal region of Venezuela (near Cumana).

Most workers have recognized two or three species in the genus, these largely circumscribed by fruit characters, but at least one worker (e.g., Rzedowski 1981, cf. discussion under *Allionia choisyi*) has recognized only a single species in the complex.

The present account is based upon the examination of approximately 1,000 herbarium specimens housed at the following institutions: ARIZ, F, GH, LL, NY, TEX, UC, US. The distributional maps (Figure 1) are based upon these collections, all of which have been annotated and serve as documentation for the study.

ALLIONIA L.

Wedelia Loeffl. 1766, not *Wedelia* Jacq. 1760.

Wedeliella Cockerell.

Annual or perennial, mostly prostrate or recumbent dichotomously branching herbs, the stems arising from slender or enlarged ligneous tap roots. Leaves opposite, simple, unequal in size. Flowers perfect in axillary panicle clusters of 3, the clusters subtended by bracts that persist and enclose the 3 fruits. Perianth in only 1 series, funnellform to rotate, pink to lavender. Stamens 4-8. Stigmas capitate. Anthocarps (fruits) with ventral (inner) surfaces rounded to flattened, the dorsal side glandular, rounded and incurved to broadly flattened, the margins with 2-8 broad to narrow teeth. Seeds with uncinat embryos.

Type species, *Allionia incarnata* L.

A widespread weedy genus with only two species, both of these partially sympatric in the drier regions of North and South America.

KEY TO SPECIES

1. Anthocarps (fruits) with ventral (inner) surfaces decidedly rounded, the dorsal side with usually 2-4 incurved deltoid to narrowly triangular teeth; stems procumbent; roots strongly perennial. *A. incarnata*
1. Anthocarps with ventral surfaces decidedly flattened, the dorsal side with usually 5-8 flattened linear-lanceolate teeth; stems strictly prostrate; roots annual or weakly perennial, sometimes strongly perennial.
..... *A. choisyi*

ALLIONIA CHOISYI Standl.

Allionia incarnata L. var. *glabra* Choisy in DC., *Prodr.* 11:435. 1849.

Wedelia glabra (Choisy) Standl., *Contr. U.S. Natl. Herb.* 12:332.

1909. *Wedeliella glabra* (Standl.) Cockerell, *Torreya* 9:167. 1909.

Allionia glabra (Choisy) Standl., *Field Mus. Publ. Bot.* 8:10. 1930.

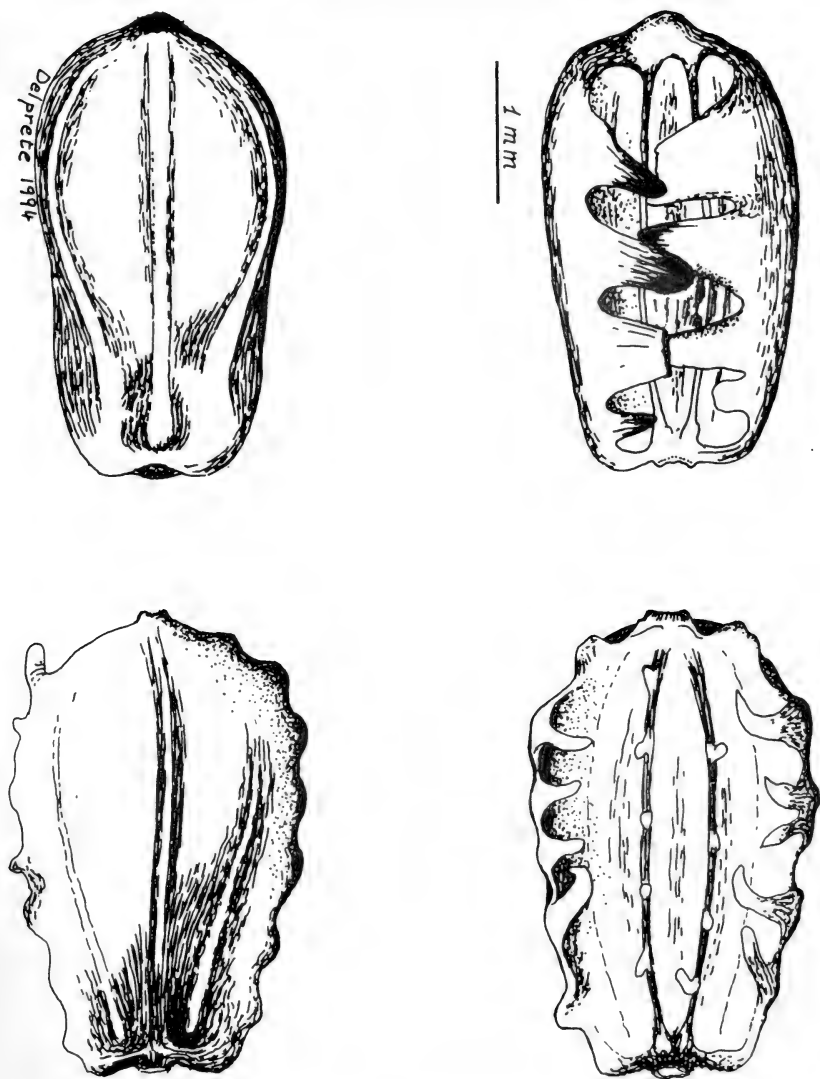


Figure 1. Fruits (anthocarps) of *Allionia choisyi* (to left) from isotype (GH) and *A. incarnata* var. *incarnata* (to right) from Perú, South America (Dillon 3215 [TEX]).

Not *Allionia glabra* (S. Wats.) O. Kuntze \equiv *Allionia choisyi* Standl., Field Mus. Publ. Bot. 8:310. 1931. TYPE: MEXICO. Tamaulipas: San Fernando, w/o date, *Berlandier 816* (pl. exs. 2236) (LECTOTYPE [selected here]: Bernhardt Herb., G-DC; Isolectotype: GH!). In his original description Choisy cited two specimens, both collected by Berlandier, one from the environs of México City (exs. 577) and one from San Fernando, Tamaulipas (exs. 2236).

Allionia incarnata L. forma *multiserrata* Heimerl in Urban, *Symb. Ant.* 7:212. 1912. TYPE: HAITI. "Prope Poste Coudan inter sexa ruderalia", 100 m, Jan w/o year, *Buch 643* (LECTOTYPE [selected here]: GZU; Isolectotype: NY!).

Allionia incarnata L. forma *glutinosissima* Heimerl, Rep. Spec. 31:97. 1939. TYPE: U.S.A. Arizona: Cochise Co., Paradise, outwash soil, camp ground, 5500 ft, 2 Oct 1907, *J.C. Blumer 1695* (HOLOTYPE: B, destroyed?; Isotypes: ARIZ!, GH!, NY!).

Annual (seemingly) or perennial herbs with markedly prostrate stems. Stems mostly slender, puberulous to puberulopilose. Larger leaves mostly 2-5 cm long, 1.2-3.5 cm wide; petioles 1-2 cm long; blades ovate to elliptic, sparsely pubescent to glabrate, the margins \pm crenulate. Flowers axillary, their pedicels slender, mostly 0.5-1.5 cm long, but often shorter. Involucral bracts ovate, mostly 3-5 mm long. Perianth mostly 3-6 mm high, pink to purple. Stamens 4-6, mostly included, 3-4 mm long. Fruits 3-5 mm long, 3-4 mm wide, flattened, the abaxial surfaces with 5-8 sharp, appressed, narrowly triangular teeth (rarely gland-tipped) along each margin, between these occur 2 rows of sticky glandular protuberances that readily adhere to the enclosing bracts.

Allionia choisyi is sympatric with *A. incarnata* (Figure 3). Vegetatively it is difficult to distinguish between these, but their fruits are markedly different, as shown in Figure 1. It is tempting to view the two taxa as but fruit forms, so similar are their habits. Standley (1909), however, took *A. choisyi* to be an annual, at least as the species occurs in "New Mexico and in other places from which I have examined specimens with roots ...". My own observations bear this out for the region concerned, but numerous plants from elsewhere having the characteristic flattened fruits of *A. choisyi* show strongly developed, apparently perennial rootstocks. *Allionia choisyi* mostly occurs in loose sandy soils while *A. incarnata* occurs in clay or silty-clay substrates, to judge from label data.

As noted under *Allionia incarnata*, Rzedowski (1951) thought *A. choisyi* to be inseparable from that species, but like most workers who have treated the two taxa, I find these to be "clear-cut" species based upon characters of the fruit; only rarely have specimens with the two fruit types been collected

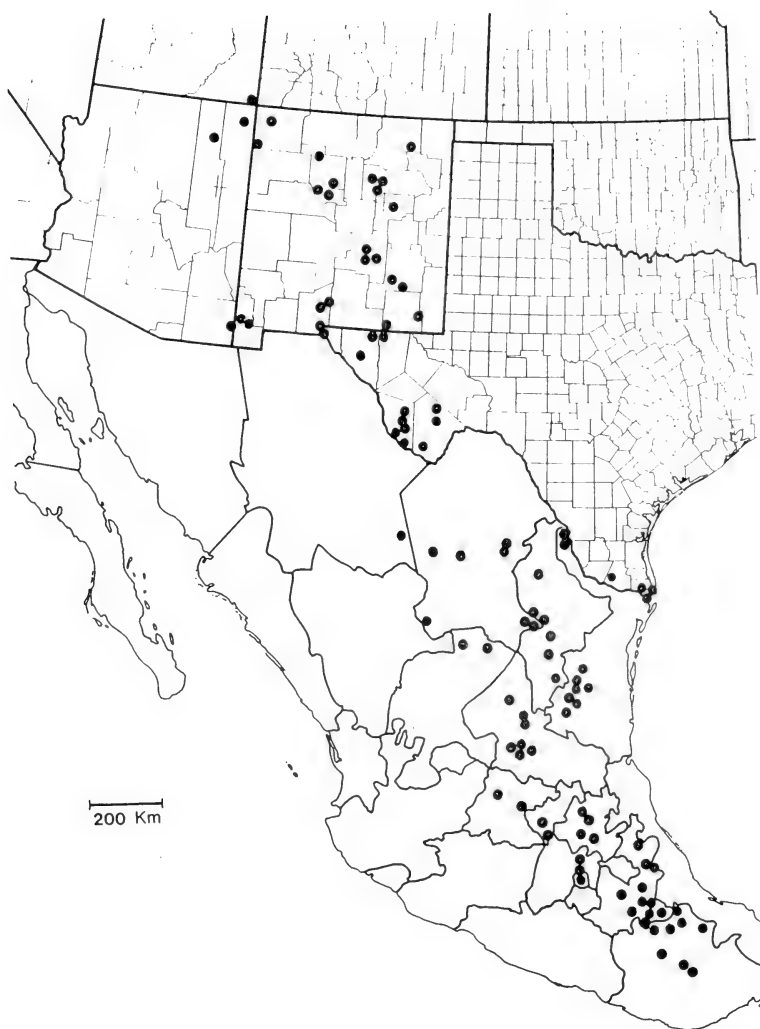


Figure 2. Distribution of *Allionia choisyi* in México and U.S.A.



Figure 3. Distribution of *Allionia choisyi* (diagonal lines and open circles) and *A. incarnata* (clear area and closed circles).

together at the same site (e.g., U.S.A. Arizona, Cochise Co., Paradise, *Blumer 1695* [*A. choisyi*] and *Blumer 1694* [*A. incarnata*]) in which case they were readily viewed as distinct by their collectors, Blumer noting that *A. choisyi* "Hugs the ground more closely than [number] 1694 with which it grows". From among the many sheets of both species which I examined truly intermediate fruits were never encountered.

Allionia incarnata f. *glutinosissima* is a small-fruited form in which the marginal teeth are gland-tipped. It occurs in an area where three taxa are known to occur within close proximity: *A. incarnata* var. *incarnata*; *A. i.* var. *villosa*, and *A. choisyi*. Perhaps complex hybridization between two or more of these taxa has produced this rather bizarre form.

Plants similar to f. *glutinosissima* occur sporadically elsewhere (e.g., vicinity of Albuquerque, New Mexico, *Rose 17800* (US) (the specimen mounted on the same sheet with a collection of *Allionia incarnata*). It is tempting to consider (in such instances) the possibility that marginal teeth with glands arise in situations of complex hybridization; alternatively *A. choisyi* might occasionally produce oddly glutinous fruit forms, throughout its range, there being a tendency for its fruits to be more glutinous than *A. incarnata*.

An excellent illustration of *Allionia choisyi* showing fruits can be found in Fay's (1980) treatment of *Allionia* for the Flora of Veracruz, albeit labeled as *A. incarnata* L.

ALLIONIA INCARNATA L., *Syst. Naturae*, ed. 10, 2:90. 1759.

Perennial herbs with procumbent or trailing stems. Stems slender or robust, variously pubescent (puberulous to villous to nearly glabrous). Larger leaves mostly 2-8 cm long, 1.5-4.5 cm wide; petioles 1-4 cm long; blades ovate or oval to obovate, variously pubescent to glabrate, the margins crenulate or undulate. Flowers axillary, their pedicels 0.5-4.0 cm long, rarely \pm sessile. Perianth mostly 4-15 mm high, pink to purple. Stamens 5-8, 4-20 mm long, mostly exserted or nearly so. Fruits 4-6 mm long, 2-3 mm wide, the adaxial portion rounded (rarely weakly so), the marginal teeth 3-4(-5), usually obtuse, rounded or nearly absent (between these 2 rows of sessile glutinous glands, rarely the glands absent).

KEY TO VARIETIES

1. Perianth mostly 8-15 mm long, at anthesis 10-20 mm across; mostly mid-elevational regions of the North American Sonoran desert west of the Continental Divide.var. *villosa*

1. Perianth mostly 4-8(-10) mm long, at anthesis 8-10(-12) mm across; widespread, in the U.S.A. mostly mid-elevational regions east of the Continental Divide or else in lower elevational zones of Sonoran desert regions. (2)
2. Anthocarps mostly 3-4 mm long; involucre mostly 4-5 mm long; Sonoran desert regions, Baja California, Sonora and closely adjacent U.S.A. var. *nudata*
2. Anthocarps mostly 4-5 mm long; involucre mostly (4-)5-7 mm long; widespread in North America mostly occurring in the Chihuahuan desert regions east of the Continental Divide southward to Hidalgo, México, also in South America. var. *incarnata*

ALLIONIA INCARNATA L. var. *INCARNATA* *Allionia incarnata* L., *Syst. Naturae*, ed. 10, 2:90. 1759. *Wedelia incarnata* (L.) Kuntze, *Rev. Gen. Pl.* 533. 1891. *Wedeliella incarnata* (L.) Cockerell, *Torreyia* 9:167. 1909. TYPE: VENEZUELA. Sucre: near Cumana, 1754, *Loefling s.n.* (HOLOTYPE: LINN).

Wedelia cristata Standl., *Contr. U.S. Natl. Herb.* 12:331. 1909. *Wedeliella cristata* (Standl.) Cockerell, *Torreyia* 9:167. 1909. *Allionia cristata* (Standl.) Standl., *Field Mus. Publ. Bot.* 8:310. 1931. TYPE: U.S.A. Arizona: Navajo Co., Holbrook, 15 Jul 1896, *Myrtle Zuck s.n.* (HOLOTYPE: US; Isotypes: NY!, US!).

Wedelia incarnata (L.) Kuntze subsp. *anodonta* Standl., *Contr. U.S. Natl. Herb.* 12:332. 1909. *Wedeliella incarnata* (L.) Cockerell var. *anodonta* (Standl.) Cockerell, *Torreyia* 9:167. 1909. TYPE: U.S.A. New Mexico: "plains of western New Mexico", Jul 1880, *Rusby 355* (HOLOTYPE: F!).

As shown in Figure 2, this is a widespread taxon in North America occurring from northern New Mexico southward throughout most of northcentral Mexico. It is also highly variable and I have been unable to distinguish North American collections from South American collections. *Allionia i.* var. *incarnata* is sympatric with *A. choisyi* in both North and South America (Figure 2). *Allionia choisyi* is readily distinguished from *A. incarnata* by its dorsally flattened anthocarps which usually possess 4-6 flattened marginal dentations, the latter mostly narrowly acute (vs. anthocarps rounded dorsally with 3-4 obtuse or rounded dentations). Nevertheless, occasional anthocarps of an intermediate nature suggest that the rare hybrid between these might occur, but I have not examined collections where the two taxa occur together with putative hybrids. According to Dr. James Henrickson (pers. comm.) populations

of *A. choisyi* from northern México are reasonably uniform morphologically, appearing quite different from those of *A. incarnata*, both in habit, flower size and color, and by substrate, *A. choisyi* preferring, in general, looser sandy soils (which might also be inferred from label data; when commented upon, *A. choisyi* is said to occur in sandy or silty stream-side soils). Jan Saunders (pers. comm.) also noted that these two taxa appear distinct in the field in South America, *A. choisyi* being much more "ground-hugging" than *A. incarnata*, the stems of which appear more nearly procumbent.

Wedelia cristata is apparently a fruit form of var. *incarnata* having an overly enlarged ventrodorsal medial ridge, otherwise it differs little, if at all, from typical elements of the latter.

***ALLIONIA INCARNATA* L. var. *NUDATA* (Standl.) Munz**

Wedelia incarnata (L.) Kuntze subsp. *nudata* Standl., Contr. U.S. Natl. Herb. 12:334. 1909. *Wedeliella incarnata* (L.) Cockerell subsp. (?) *nudata* (Standl.) Cockerell, Torreya 9:167. 1909. *Allionia incarnata* L. var. *nudata* (Standl.) Munz, *California Fl.* 391. 1959. TYPE: U.S.A. California: Coyote Canyon, ca. 1540 m, 1902, *E. Hall* 2799 (HOLOTYPE: UC!).

Allionia malacoides Benth., Bot. Voy. Sulphur 44. 1844. TYPE: MEXICO. Baja Calif.: w/o locality, 1836-1842, *Barclay & Hinds s.n.* (HOLOTYPE: BM).

This taxon was apparently first described (at the species level) by Bentham in 1844, from material collected in Baja California, as noted in the above synonymy. It is largely distinguished from the allopatric var. *villosa* by its habit (seemingly annual or weakly perennial, the leaves relatively remote) and small perianths.

***ALLIONIA INCARNATA* L. var. *VILLOSA* (Standl.) B.L. Turner, comb. nov. BASIONYM: *Wedelia incarnata* (L.) Kuntze subsp. *villosa* Standl., Contr. U.S. Natl. Herb. 12:333. 1909. *Wedeliella incarnata* (L.) Cockerell var. (?) *villosa* (Standl.) Cockerell, Torreya 9:167. 1909. TYPE: U.S.A. Arizona: "Mesas and Foothills", 22 May 1881, *C.G. Pringle s.n.* (HOLOTYPE: MO; Isotypes: GH!, NY!).**

This taxon is weakly differentiated from var. *incarnata* and is largely distinguished from the latter by its generally more robust habit, longer pedicels, and larger perianths with elongate anthers, as emphasized by Standley in his original description. Such large-flowered forms are seemingly restricted

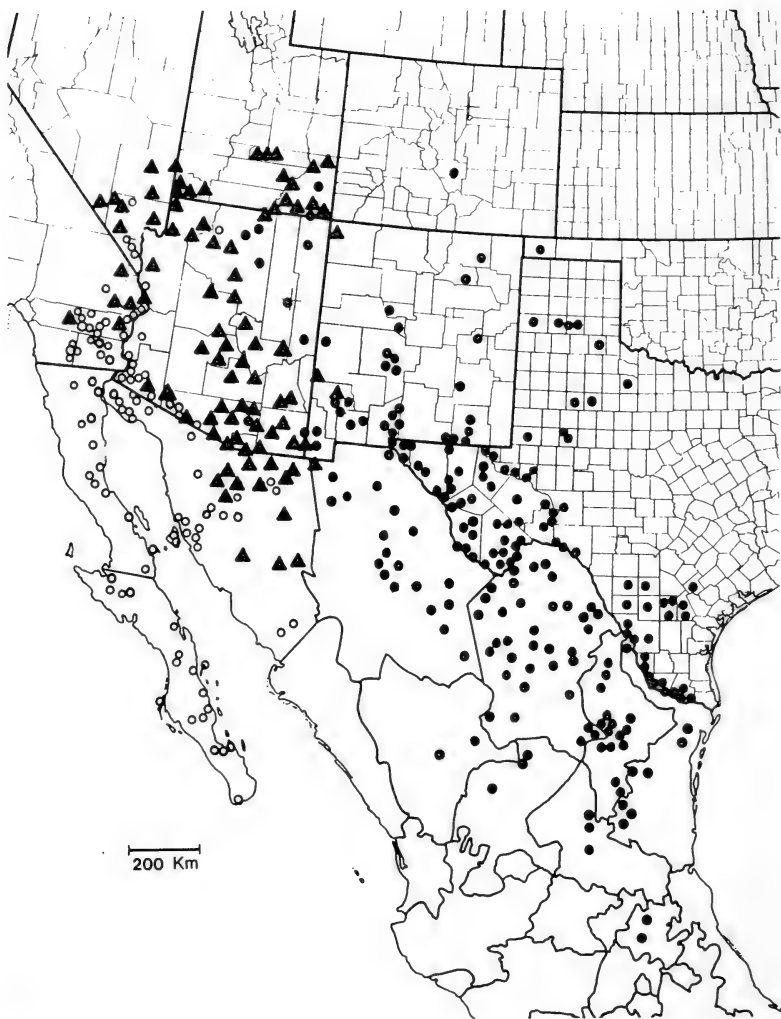


Figure 4. Distribution of *Allionia incarnata* in México and U.S.A.: *var. incarnata* (closed circles); *var. nudata* (open circles); and *var. villosa* (triangles).

to the northwestern portions of the Sonoran desert, standing between the small-flowered var. *nudata* to the west and the somewhat variable but also small-flowered var. *incarnata* to the east, as shown in Figure 2. Still, had the taxon not already been provided with a name, I would have not been hesitant to provide one since the combination of characters which mark it seem largely confined to Arizona and closely adjacent regions. Nevertheless, intermediates between var. *villosa* and var. *nudata* occur in regions of overlap, or near overlap.

ACKNOWLEDGMENTS

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TAXONOMIC TREATMENT OF *MONARDA* (LAMIACEAE) FOR TEXAS AND MEXICO

B.L. Turner

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

A taxonomic treatment of *Monarda* for Texas and México is rendered. In Texas eighteen taxa in eleven species are recognized: *M. citriodora*, with two infraspecific categories, var. *citriodora*, and var. *parva*; *M. clinopodioides*; *M. fistulosa*, with two infraspecific categories, var. *menthifolia* and var. *mollis*; *M. fruticulosa*; *M. lindheimeri*; *M. maritima* (Cory) B.L. Turner, *comb. nov.*; *M. pectinata*; *M. punctata*, with five infraspecific categories, var. *correllii* B.L. Turner, *var. nov.*, var. *intermedia*, var. *lasiodonta*, var. *occidentalis*, and var. *punctata*; *M. russeliana*; *M. stanfieldii*; and *M. viridissima*. In México nine taxa in seven species are recognized: *M. bartlettii* (including *M. dressleri* and *M. malloryi*); *M. citriodora*, with two infraspecific categories, var. *austroromontana* (Epling) B.L. Turner, *comb. nov.* (including *M. mexicana*) and var. *citriodora* (including var. *attenuata*); *M. eplingiana*; *M. fistulosa*; *M. pectinata*; *M. pringlei*; and *M. punctata*, with two infraspecific categories, var. *correllii* and var. *occidentalis*. A key to the taxa of both regions is presented, along with relevant synonymy, and distributional maps for the species concerned.

KEY WORDS: Lamiaceae, *Monarda*, Texas, México

A forthcoming treatment of the Lamiaceae of Texas has prompted the present paper. One might think that the genus *Monarda*, which is an abundant roadside weed over most of Texas, would have been adequately studied taxonomically, especially since two inclusive systematic treatments of the genus by well-trained workers have appeared within the last 55 years (McClintock & Epling 1942; Scora 1967). The presentation by McClintock & Epling was produced from only a smattering of collections from Texas and México, and was mostly accomplished without field work. The study by Scora largely followed

the nomenclature of McClintock & Epling but did include a summer or two of field work and some experimental studies. Nevertheless, neither of these taxonomic treatments are fully acceptable to me, largely because their biological concepts as to what a species or infraspecific category might be is at variance with mine, which I have opined upon in more detail elsewhere (Turner 1994).

This present study is based upon the examination of a large suite of specimens at LL, TEX (over 2,000 sheets), supplemented by the loan of selected specimens from the following institutions (BH, CAS, NY, UC, US). The distributional maps (Figures 1-7) are largely based upon these specimens, all of which have been annotated and are easily available to workers who might wish to question this or that occurrence.

Key to Texas species of *Monarda*

1. Flower clusters single and terminal (very rarely two); stamens exserted beyond upper lip. (2)
1. Flower clusters two or more, both axillary and terminal (rarely 1 on depauperate plants); stamens not exserted. (5)
 2. Corollas white to pale pink, the lower lips markedly red-spotted; mid-stem leaves with petioles mostly 1-3 mm long; plants of border areas of northeastern Texas. 12. *M. russeliana*
 2. Corollas white to pale lavender, the lower lips not markedly red-spotted; midstem leaves with petioles 3 mm long or more. (3)
3. Corollas deep pink to lavender; trans-Pecos Texas.
..... 5a. *M. fistulosa* (var. *menthifolia*)
3. Corollas white to pale pink to pale lavender; eastern Texas. (4)
 4. Corollas white; midstem leaves with petioles mostly 3-7 mm long, or if somewhat longer then to some extent pilose with spreading hairs.
..... 7. *M. lindheimeri*
 4. Corollas pale pink to pale lavender; midstem leaves with petioles mostly 8 mm long or more, never pilose with spreading hairs.
..... 5b. *M. fistulosa* (var. *mollis*)
5. Leaves linear, mostly 1-3 mm wide, densely and evenly minutely appressed-strigose throughout, the foliage ashy-white; southernmost Texas.
..... 6. *M. fruticulosa*
5. Leaves variously lanceolate, mostly 4 mm wide or more, variously pubescent but not as described in the above. (6)

6. Suffrutescent sprawling shrublets or shrubs to 1 m high; stems with spreading pilose hairs 1-2 mm long; southernmost coastal Texas (Kleberg to Refugio counties). 8. *M. maritima*
6. Annual or stiffly erect perennial herbs, never shrublets or shrubs; stems w/o pilose hairs 1-2 mm long. (7)
7. Leaves (of primary stems) linear-lanceolate, mostly 4-6 mm wide; stems with vestiture of short hairs spreading at right angles to stem (rarely downcurved); mostly Carrizo sands of southcentral Texas. 14. *M. viridissima*
7. Leaves lanceolate-ovate to ovate, mostly 7 mm wide or more; stems with vestiture various, mostly down-curved but not as described in the above; widespread. (8)
8. Calyx lobes variously deltoid, 1-3 times as long as wide. (9)
8. Calyx lobes narrowly subulate or attenuate to awned, (3-)5-10 times as long as wide (including awns). (10)
9. Calyx mouth manifestly closed by a dense mass of white hairs arising at its orifice; tube of corolla glabrous; central mineral region of Texas and closely adjacent areas in granite or sandy soils, mostly along the Colorado River or its tributaries. 13. *M. stanfieldii*
9. Calyx mouth not as described in the above, the orifice merely ciliate; tube of corolla pubescent; widespread. 11. *M. punctata*
10. Bracts of floral clusters mostly elliptical to oblanceolate, abruptly narrowed into a bristle-tip. 2. *M. citriodora*
10. Bracts of floral clusters lanceolate, gradually tapering into a terminal bristle. (11)
11. Bracts and calyx lobes mostly purplish; corollas purplish; plants mostly 30-60 cm high. 3. *M. clinopodioides*
11. Bracts and calyx lobes mostly greenish; corollas yellowish to creamy white; plants mostly 20-40 cm high. 9. *M. pectinata*

Key to Mexican species of *Monarda*

1. Flower clusters terminal, nearly always 1 head to a stem. (2)
1. Flower clusters both terminal and axillary, nearly always 2 or more heads to a stem. (5)

- 2. Corollas red or purple-red. (3)
- 2. Corollas white, pink or pale lavender. 5. *M. fistulosa*
- 3. Calyx teeth mostly 1-2 mm long, 1-2 times as long as wide; northern Coahuila. 4. *M. eplingiana*
- 3. Calyx teeth mostly 2-4 mm long, 3-4 times as long as wide; Nuevo León and Tamaulipas, south to Veracruz. (4)
 - 4. Corollas bright red; calyx teeth mostly (2.0-)2.5-3.5 mm long; mountains near Monterrey, Nuevo León. 10. *M. pringlei*
 - 4. Corollas rosy-red to lavender-red; calyx teeth mostly 2.0-2.5 mm long; Gulf Coastal slopes of Sierra Madre Oriental from Tamaulipas to Veracruz. 1. *M. bartlettii*
- 5. Calyx lobes deltoid, 1-2 times as long as wide. 11. *M. punctata*
- 5. Calyx lobes narrowly subulate, or attenuate to awned, (3-)5-10 times as long as wide. (6)
 - 6. Bracts of floral clusters mostly elliptical to oblanceolate, abruptly narrowed into a bristle-tip. 2. *M. citriodora*
 - 6. Bracts of floral clusters lanceolate, gradually tapering into a terminal bristle. (7)
- 7. Plants mostly 20-40 cm high; corollas purplish. 2. *M. citriodora*
- 7. Plants mostly 30-60 cm high; corollas creamy-white to yellowish.
 - 9. *M. pectinata*

1. *MONARDA BARTLETTII* Standley, Field Mus. Publ. Bot. 17:208. 1937. TYPE: MEXICO. Tamaulipas: La Vagonia, vicinity of San José, 3200 ft, 5 Jul 1930, *H.H. Bartlett 10094* (HOLOTYPE: F!).

Monarda malloryi Gilly, Bull. Torrey Bot. Club 17:658. 1944. TYPE: MEXICO. Veracruz: near Piletas, 14 Jul 1943, *D. Dodds 105* (HOLOTYPE: NY!).

Monarda dressleri Scora, Madroño 18:199. 1965. TYPE: MEXICO. Tamaulipas: Mpio. Aldama, region of Rancho Las Yucas, ca. 40 km W of Aldama, 16 Jul 1957, *Dressler 1851* (HOLOTYPE: MEXU; Isotypes: MICH, UC!).

This taxon is exceedingly close to *Monarda pringlei* Fernald and might be reduced to varietal rank under the latter without much ado. It is retained at the species level following the studies of both McClintock & Epling (1942) and Scora (1967). The latter also retained both *M. malloryi* and *M. dressleri* on the basis of morphological minutia that I have been unable to affirm. The type of *M. bartlettii* differs from most collections of the species in northeastern México in having somewhat larger, more pubescent leaves.

2. *MONARDA CITRIODORA* Cerv. ex Lag., *Gen. Sp. Nov.* 2. 1816. TYPE: MEXICO. w/o locality [plants grown from seeds sent to Madrid in 1814 by Cervantes]. According to Epling (1942) "What are apparently authentic specimens, distributed by Pavon, are in ..." BM and G-DC. Epling notes (having examined these), that "The Pavon specimens are very similar to specimens from northeastern México, where perchance the original seeds were obtained by Cervantes or his colleagues at the time concerned" (LECTOTYPE [selected here]: BM!; Isolectotype: G-DC).

This is a widespread highly variable species as noted by McClintock & Epling (1942) and Scora (1967). The former workers recognized *Monarda citriodora*, *M. austromontana* Epling and *M. mexicana* Epling as good species, while Scora (1967) recognized only the latter as distinct, reducing *M. austromontana* to subspecific rank. I recognize only three varieties under the *M. citriodora* species-complex, as follows:

Key to varieties of *Monarda citriodora*

1. Apical portion of upper lip of corolla pubescent with inconspicuous appressed hairs mostly 0.1-0.5 mm long; Sierra Madre of western México and western U.S.A. var. *austromontana*
1. Apical portion of upper lip of corolla pubescent with few to numerous conspicuous long erect or spreading hairs 0.8-1.7 mm long; eastern México and adjacent U.S.A. (2)
 2. Calyx tubes mostly 5-7 mm long; corolla tubes 8-11 mm long; coastal region of southern Texas. var. *parva*
 2. Calyx tubes mostly 7-15 mm long; corolla tubes 11-18 mm long; widespread. var. *citriodora*

2a. *MONARDA CITRIODORA* Cerv. ex Lag. var. *CITRIODORA*

Monarda citriodora Cerv. ex Lag. subsp. *citriodora*.

Monarda aristata Nutt. (1837).

Monarda dispersa Small (1903).

Monarda tenuiaristata A. Gray ex Small (1903).

Monarda citriodora Cerv. ex Lag. var. *attenuata* Scora, Madroño 18:121.

1965. TYPE: MEXICO. Coahuila: near Musquiz, 1963, R.W. Scora 2340 (HOLOTYPE: MICH; Isotype: UCR).

The typical infraspecific element of *Monarda citriodora*, as indicated in the above account, is said to be typified by material at BM and G-DC, examined by Epling. The latter worker thought type material applied to the widely distributed taxon of eastern North America, Epling himself having proposed the more western taxon, var. *austromontana* (Epling) B.L. Turner (first as a species [Epling 1935], but subsequently reduced to a subspecies [Scora 1965]).

I can not recognize Scora's var. *attenuata*. He contends (1967) that "Variety *attenuata* is distinguishable by its horizontally spreading bracts, the nearly glabrous adaxial bract surfaces, green coloration, and more attenuate bract apices. The calyx lobes have a few or no lateral pili [long hairs] and the average corolla dimensions are larger than those of var. *citriodora*." All of these characters are exceedingly variable, both among the populations in northern México (numerous collections now on hand at LL, TEX, not examined by Scora), as well as among and within populations in the U.S.A. The only character called to the fore by Scora that appears to have any regional reliability is that of corolla size, for the populations in northern México do tend to have larger corollas (mainly more pronounced upper and lower lips) than do most collections from the U.S.A. However, exceptions to this generality abound within populations of both regions.

2b. *MONARDA CITRIODORA* Cerv. ex Lag. var. *AUSTROMONTANA* (Epling) B.L. Turner, *comb. nov.* BASIONYM: *Monarda austromontana* Epling, Madroño 3:29. 1935. *Monarda citriodora* Cerv. ex Lag. subsp. *austromontana* (Epling) Scora, Madroño 18:120. 1965. TYPE: MEXICO. Chihuahua: La Bufa Mountain, near Cusihiuriachic, 2 Sep 1887, C.G. Pringle 1955 (HOLOTYPE: US!; Isotypes: F!, US!).

Monarda mexicana Epling, Madroño 3:26. 1935. TYPE: MEXICO.

Durango: w/o locality, w/o date, P.I. Garcia 399 (HOLOTYPE: US!).

This variety, like var. *citriodora*, is a relatively common, widely distributed, exceedingly variable taxon. It was largely distinguished from var. *citriodora* by its "lanceolate to linear-lanceolate" glomerular bracts which were said to be "not more than 4 mm wide", gradually acuminate apically, and strongly reflexed from the base. While this is true for most of the specimens examined by myself (for distribution cf. Figure 1), there are numerous exceptions to this generality, especially among recent collections from Durango along highway 40 between the cities of Durango and Mazatlán (but also elsewhere in the state of Chihuahua, LL-TEX). Not only are the bracts remarkably variable as to size, shape, indument, and color, there is also considerable variation as to the size and pubescence of calyx lobes. Indeed, I view *Monarda mexicana* to be a name bestowed upon forms of var. *austromontana* having somewhat trianguloid calyx lobes. For example, there is no doubt in my mind that Scora's citation of *Maysilles* 7771 (TEX,US) as belonging to his concept of *M. mexicana*, occurring along the Durango-Mazatlán highway, is but a collection of *M. c.* var. *austromontana* with reduced calyx lobes such as occurs on the type of *M. mexicana*. The plants concerned occur among a bevy of highly variable populations in this region, all with mostly elongate calyx lobes (and broad to narrow bracts) and are easily referable to Scora's subsp. *austromontana*. The exact locality in Durango of type material for *M. austromontana* is not known, but from my own experience with collections obtained by Mr. Garcia, this is likely to have been collected in the montane regions of northwesternmost Durango or possibly closely adjacent northern Sinaloa.

The var. *austromontana* was distinguished from var. *citriodora* by Scora largely because of its narrower glomerular bracts. I find glomerular bracts, especially in the former taxon, sufficiently variable so as to be unconvincing as diagnostic characters, as noted in the above account. The best character I found to distinguish between the two taxa is that of upper-lip pubescence of the corolla (as shown in my key), although, in general, var. *austromontana* is a smaller plant, having smaller glomerules and smaller bracts than var. *citriodora*. As can be seen by the distribution map of *M. citriodora* (Figure 1), its two large regional varieties are well separated, but characters which mark these do vary in peripheral populations, one toward the other, but not to any large extent, and one might say that the two varieties have achieved subspecific status, much as indicated by Scora.

- 2c. *MONARDA CITRIODORA* Cerv. ex Lag. var. *PARVA* Scora, Madroño 18:120. 1965. TYPE: U.S.A. Texas: San Patricio Co., near Sinton, C.M. Rowell 4977 (HOLOTYPE: WWF).

This name has been applied to localized populations along the Gulf Coastal regions of southern Texas (Figure 3) which mostly occur in heavy clay soils and

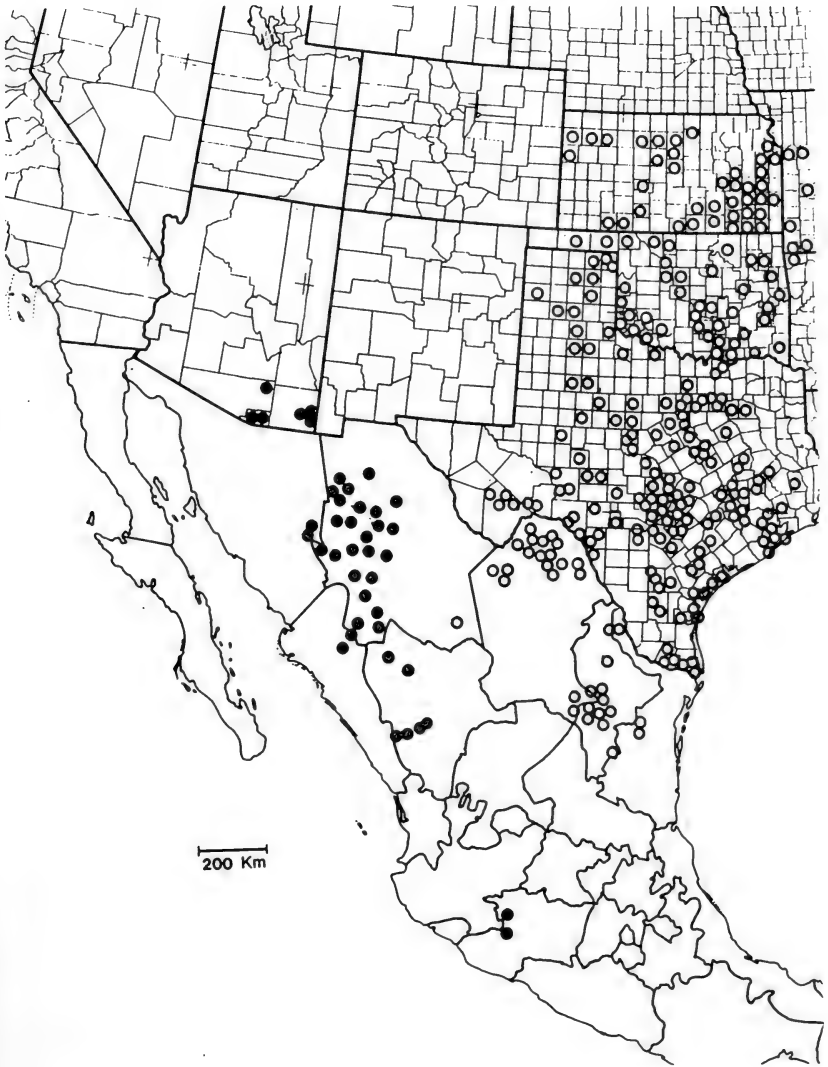


Figure 1. Distribution of *Monarda citriodora* var. *citriodora* (open circles); and var. *austromontana* (closed circles). Variety *parva* not shown, for which see Figure 3.

are apparently "fixed" in their genetic proclivity for the production of reduced flowers (Scora 1965). Such "forms" were first called to the fore by McClintock & Epling (1942, p. 192), as noted by Scora in his formalized description of the taxon.

3. *MONARDA CLINOPODIOIDES* A. Gray, *Syn. Fl. N. Amer.* 2:375. 1878.

TYPE: U.S.A. Texas: Dallas Co., near Dallas, Jun 1874, *J. Reverchon s.n.* (LECTOTYPE [selected by Scora 1967]: GH).

Monarda aristata Hook., Hook. Bot. Mag., pl. 3526. 1836. TYPE:

U.S.A. Texas: described from plants grown in London, the seeds from southcentral Texas, probably from what is now Austin Co., 1833-1834, *T. Drummond s.n.* (HOLOTYPE: K). \equiv *Monarda citriodora* Cerv. ex Lag. var. *aristulata* A. Gray, Proc. Amer. Acad. Arts 8:369. 1873. (lacking a specimen at K, the plate represents adequate typification). Not *Monarda aristata* Nutt.

Monarda clinopodioides is similar to *M. pectinata* Nutt., but in Texas these have quite different distributions (Figure 3 and Figure 6), although McClintock & Epling (1942) cite two questionable specimens of the latter from central Texas which I take to be misidentifications or possibly, adventive weeds in this region.

4. *MONARDA EPLINGIANA* Standley, Field Mus. Publ. Bot. 17:208. 1937.

TYPE: MEXICO. Coahuila: Del Carmen Mts., Vivoras Canyon, 9000 ft, 26 Aug 1936, *E.G. Marsh, Jr.* 604 (HOLOTYPE: F!; Isotype: TEX!).

This taxon is closely related to *Monarda pringlei* and was treated as synonymous with the latter by McClintock & Epling (1942). Scora (1967), however, recognized the species, distinguishing it from *M. pringlei* by its supposedly thinner ovate to ovate-lanceolate (vs. lanceolate), long-petiolate leaves ("5-8 mm long" vs. "4-9 mm") and calyx lobes with glandular processes sessile or absent (vs. numerous and stalked). I find all of these "key" characters to be quite variable but can discern that *M. eplingiana*, confined to northcentral Coahuila (Figure 2), is perhaps worthy of recognition. The most consistent character I find to distinguish between these are those of the calyx, *M. eplingiana* possessing shorter, broader lobes (mostly 1.0-1.5 mm long vs. 2.5-3.5 mm long).

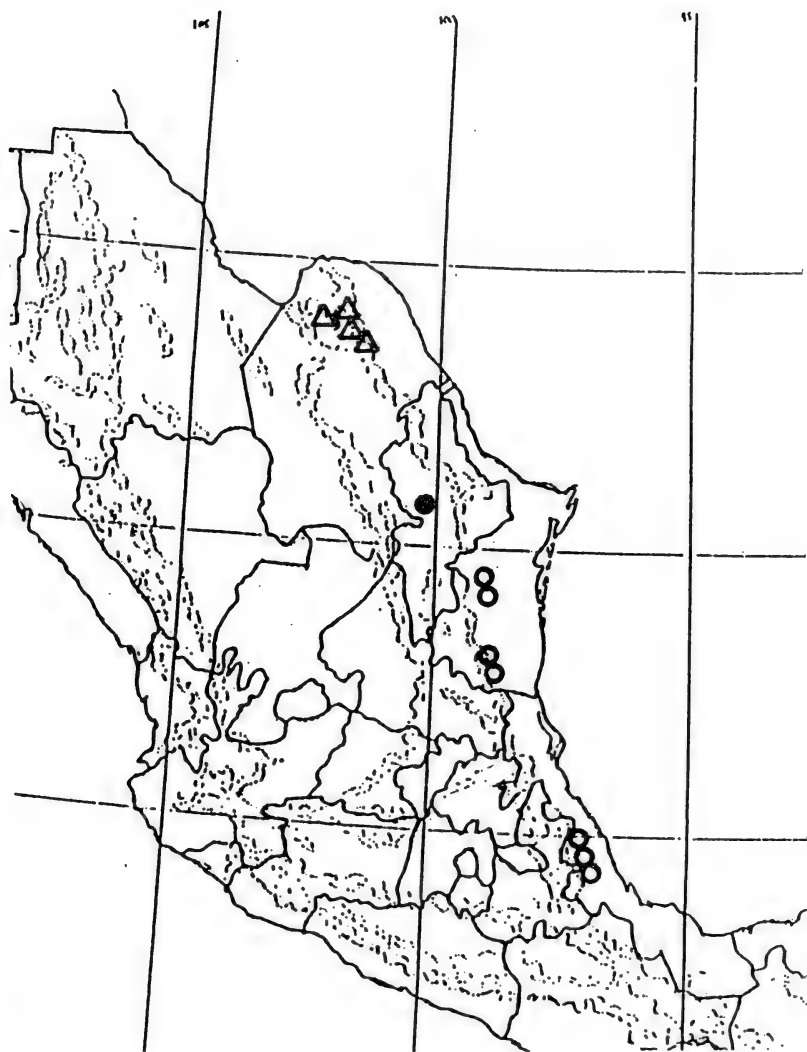


Figure 2. Distribution of *Monarda bartlettii* (open circles); *M. eplingiana* (open triangles); and *M. pringlei* (closed circle).

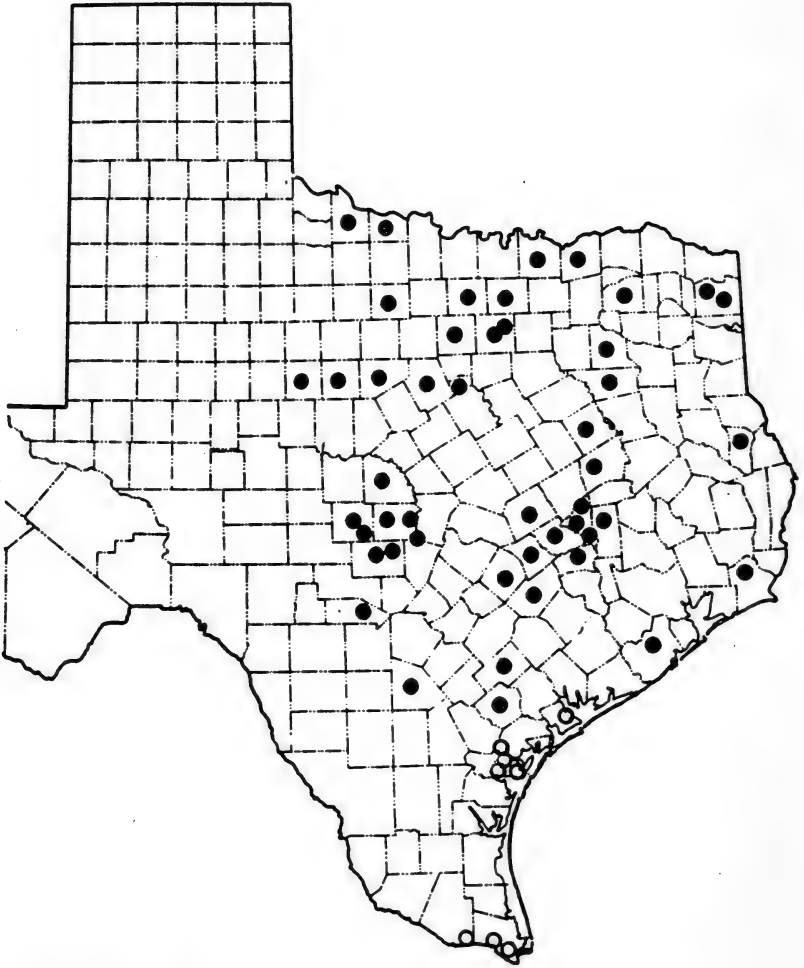


Figure 3. Distribution of *Monarda clinopodioides* (closed circles) in Texas; and *M. citriodora* var. *parva* (open circles).

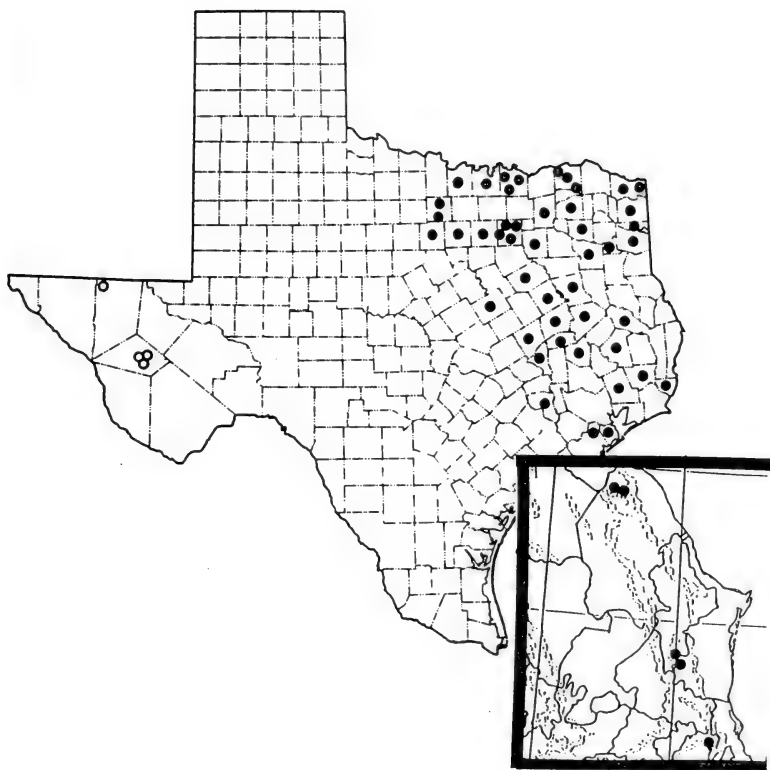


Figure 4. Distribution in Texas of *Monarda fistulosa* var. *menthifolia* (open circles), and var. *mollis* (closed circles); inset, var. *menthifolia* in México (closed circles).

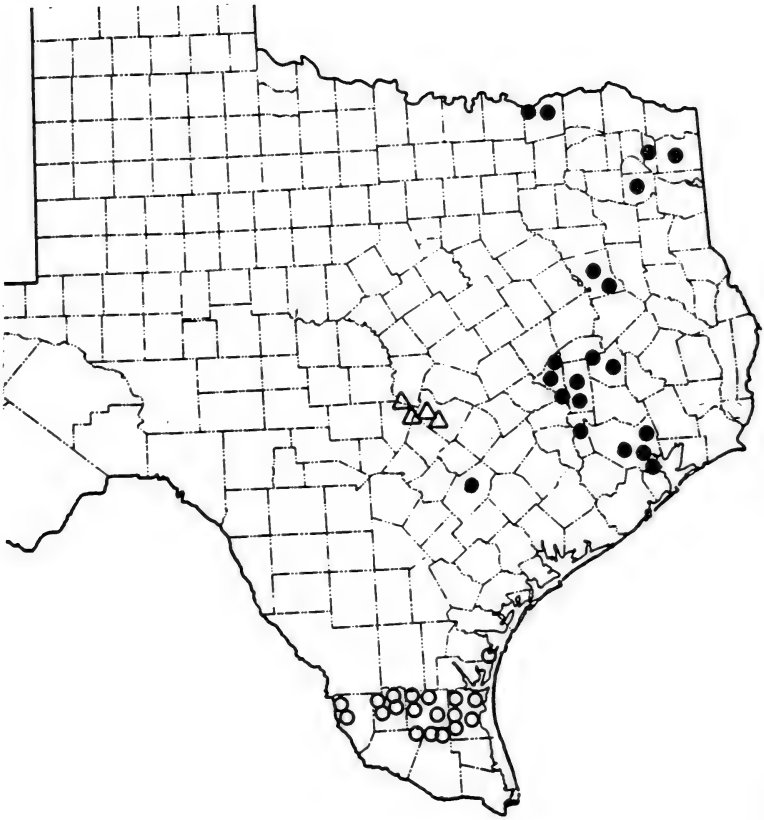


Figure 5. Distribution of *Monarda fruticulosa* (open circles); *M. lindheimeri* (closed circles); and *M. stanfieldii* (open triangles).

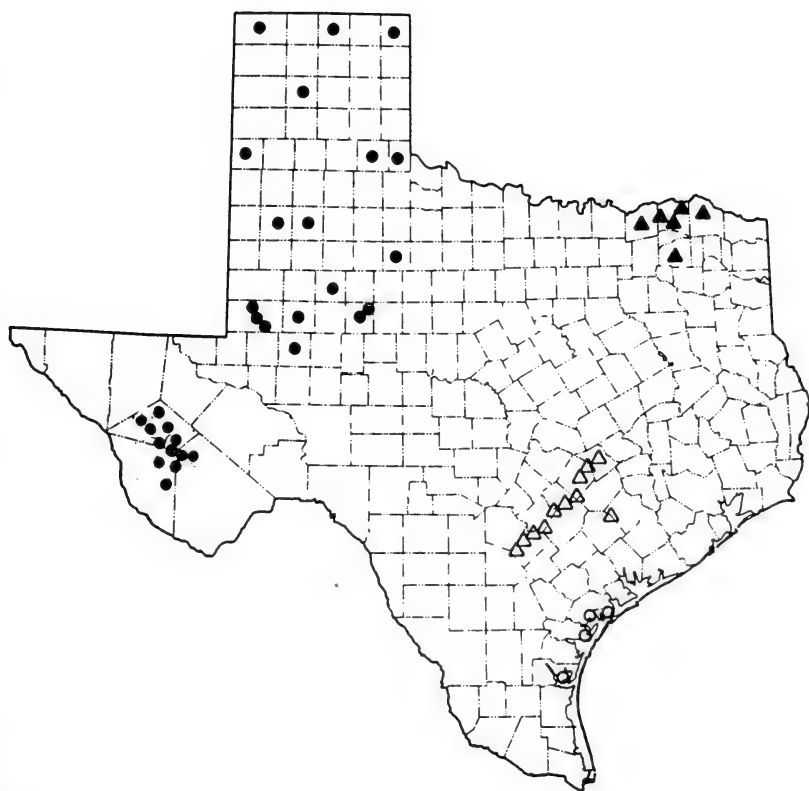


Figure 6. Distribution of *Monarda maritima* (open circles); *M. pectinata* (closed circles) in Texas; *M. russeiana* (closed triangles) in Texas; and *M. viridissima* (open triangles).

5. *MONARDA FISTULOSA* L., *Sp. Pl.* 1:22. 1753.

This is a widespread highly variable species of temperate North America. Several workers have recognized two or more regional varieties in the complex (e.g., Fernald 1950; McClintock & Epling 1942; Fosberg & Artz 1953). The var. *fistulosa* is thought to be largely confined to the upper New England states. Those taxa occurring in Texas and México are var. *mollis* (L.) Benth. and var. *menthifolia* (Graham) Fernald. Fosberg & Artz (1953) provided an adequate overview of the complex noting that var. *menthifolia* is distinguished from var. *mollis* by "its stiffer and mostly simpler ... lower stems and shorter-petioled leaves, ... into which it passes insensibly in the eastern part of the range." Following most workers, I also recognize but two regional varieties of *M. fistulosa* as occurring in Texas. These can be recognized by the following couplet:

1. Stems simple, rarely branched; midstem leaves with petioles mostly 2-8 mm long; trans-Pecos Texas and México. var. *menthifolia*
1. Stems tall and branched; midstem leaves with petioles mostly 8-30 mm long; eastern Texas and eastern U.S.A. var. *mollis*

- 5a. *MONARDA FISTULOSA* L. var. *MENTHIFOLIA* (Graham) Fernald, *Rhodora* 46:495. 1944. BASIONYM: *Monarda menthifolia* Graham, *Edin. New Phil. J.* 387. 1829. *Monarda fistulosa* L. subsp. *menthifolia* (Graham) L.S. Gill, *Caryologia* 30:787. 1984. TYPE: CANADA. Saskatchewan: "Norway House on the Saskatchewan River", 1825-1827, *Drummond s.n.* (HOLOTYPE: CL). Type material grown in Edinburgh, Scotland, from seed provided by Drummond (Epling 1942).

As indicated in the above, this is the westernmost variety of *Monarda fistulosa*. Epling (1942) treated the taxon at the specific level, but Scora (1967) accepted it as varietally distinct and largely confined to the western U.S.A. and Canada.

Scora does not report collections of this taxon from México, but I have examined the following: Coahuila: *Henrickson 11428, 11658* (LL); *Johnston et al. 11792A* (TEX). Nuevo León: *Hinton et al. 22142, 23204* (TEX). Tamaulipas: *McDonald 676.5* (TEX). Scora cited two collections of var. *mollis* from Hidalgo, México, which I have not examined, but I think these are better treated as var. *menthifolia*, to judge from other collections from this region (cf. Figure 4).

- 5b. *MONARDA FISTULOSA* L. var. *MOLLIS* (L.) Benth., *Lab. Gen Sp.* 317. 1933. BASIONYM: *Monarda mollis* L., *Amoen. Acad.* 3:399. 1756. TYPE: U.S.A. collection date and locality unknown, but probably from the southeastern states; described from material grown in the garden of Linnaeus (HOLOTYPE: LINN).

This taxon is relatively rare in easternmost Texas but is widespread in the eastern U.S.A. (cf. McClintock & Epling 1942, Figure 8). I surmise, based on McClintock & Epling's (1942) treatment and from my own examination of a wide set of specimens, that var. *mollis* will ultimately be subsumed under the var. *fistulosa*, there being little morphogeographical coherence of the characters used to distinguish between these.

6. *MONARDA FRUTICULOSA* Epling, *Madroño* 3:26. 1935. *Monarda punctata* L. var. *fruticulosa* (Epling) Scora, *Univ. Calif. Publ. Bot.* 41:46. 1967. TYPE: U.S.A. Texas: Duval Co., near Pena Station, Sep 1884, *Havard s.n.* (HOLOTYPE: US).

This is a well-marked shrub or shrublet to 1 m high, confined to south Texas (Figure 5) and readily recognized by its very narrow ashen leaves and markedly villous calyces. Scora (1967) gives little reason for its reduction to varietal status. McClintock & Epling (1942) retained the species, although they noted that "This proposed species may prove to be confluent with *M. p.* subsp. *immaculata* [= *M. punctata* var. *lasiodonta*]." I found no evidence that these two taxa might pass one into the other, nor did Scora provide any.

7. *MONARDA LINDHEIMERI* Engelm. & A. Gray, *Boston J. Nat. Hist.* 5:228. 1847. TYPE: U.S.A. Texas: Harris Co., near Houston, 1843, *F. Lindheimer 151* (HOLOTYPE: GH).

Monarda hirsutissima Small, *Fl. S.E. U.S.* 1037, 1903. TYPE: U.S.A. Texas: w/o collector or date (HOLOTYPE: Chapman Herbarium, NY!); McClintock & Epling (1942) thought it "highly probable" that the type sheet cited by Small was a Carpenter collection from Opelousas, Louisiana (PH), although Small gave the locality as Texas.

Monarda lindheimeri is closely related to *M. fistulosa*, but was maintained by both McClintock & Epling (1942) and Scora (1967). The latter worker noted that *M. lindheimeri* is "easily" distinguished from *M. fistulosa* var. *mollis* (with which it is sympatric, Figures 5 and 4) by its "lax and branched glomerules, by its sharp-angled stems with pigmented lines along the edges,

and by its shorter petioles and more ovate leaves". It is likely that the occasional hybrid between these two taxa occurs, as also suggested by Scora (1967).

8. **MONARDA MARITIMA** (Cory) B.L. Turner, *comb. nov.* BASIONYM:
Monarda punctata L. var. *maritima* Cory, Field & Lab. 17:52. 1949.
TYPE: U.S.A. Texas: San Patricio Co., 4 mi W of Aransas Pass, 14
Oct 1951, *F.B. Jones 648* (HOLOTYPE: SMU).

Shinners (1953) and Scora (1967) retained this well-marked taxon at the varietal level. I have no hesitation in recognizing its specific status, the taxon essentially confined to the deep sandy soils of southern Texas (Figure 6) and does not appear to intergrade with any of the several other *Monarda* taxa in this area, although the occasional hybrid between these might be expected.

9. **MONARDA PECTINATA** Nutt., J. Acad. Phil., ser. 2, 1:182. 1847.
TYPE: U.S.A. New Mexico: Santa Fe Co., near Santa Fe, w/o date,
Gambel s.n. (HOLOTYPE: K, according to McClintock & Epling 1942).

This is a widespread variable species of the short grass prairie regions of southcentral U.S.A. It might be confused with *Monarda citriodora* var. *citriodora*, but the latter is a more eastern plant, having larger glomerules, and more expanded, more abruptly contracted glomerular bracts. In Texas the occasional hybrid probably occurs between *M. pectinata* and *M. citriodora*, at least what appear to be putative hybrids (e.g., *Young s.n.*, 9 Sep 1918, TEX, so annotated by Epling) occur in trans-Pecos, Texas (Jeff Davis Mts.), where the two taxa occur together or within close proximity (*cf.* Figure 6 and Figure 1).

Monarda pectinata appears to be morphologically more or less intermediate between *M. citriodora* var. *austromontana* and *M. c.* var. *citriodora*. Indeed, I suspect that *M. pectinata* might be treated as an intergrading allopatric variety within the *M. citriodora* complex without much complaint from the field-oriented systematist, for it appears to intergrade with *M. citriodora* var. *austromontana* in northern México and closely adjacent areas of the U.S.A. This surmise is not addressed here because of time constraints and the need for detailed field work in the area concerned to test the surmise.

10. **MONARDA PRINGLEI** Fernald, Proc. Amer. Acad. Arts 36:501. 1901.
TYPE: MEXICO. Nuevo León: near Monterrey, Jul 1888, *C.G. Pringle 2199* (HOLOTYPE: GH).

This attractive taxon is closely related to both *Monarda eplingiana* and *M. bartlettii* and all of these might be combined without much ado. *Monarda pringlei* is apparently confined to the higher more mesic montane sites in the vicinity of Monterrey, *M. eplingiana* to the more mesic sites of the Sierra Del Carmens of northern Coahuila, while *M. bartlettii* has a wider distribution, occurring at relatively low elevations in cloud forests along the front ranges of the Sierra Madre Oriental (Figure 2).

11. *MONARDA PUNCTATA* L., *Sp. Pl.* 1:22. 1753. TYPE: U.S.A. locality, collection date, and collector unknown (HOLOTYPE: L, according to Epling 1935).

This is a widespread variable species of the eastern portions of North America. McClintock & Epling (1942) treated the species as having eight subspecies, the typical subspecies largely confined to the Atlantic and Gulf Coastal regions of the U.S.A. Scora (1967) maintained all of these taxa, adding three additional ones, bringing to eleven the number of infraspecific taxa recognized. Scora treated all of these at the varietal level; nine of the eleven were said to occur in Texas. I have treated four of Scora's varieties as species (*M. fruticulosa*, *M. maritima*, *M. stanfieldii* Small, and *M. viridissima* Correll), believing these to be sympatric with *M. punctata* (s.l.), each occupying a restricted ecogeographic region and none showing intergradation with the various infraspecific taxa of *M. punctata*, although this is not to say that the occasional interspecific hybrid might not be found in regions of sympatry where this or that taxon occur together or in close proximity. Four of Scora's Texas varieties are recognized in addition to a fifth, var. *correllii*, newly described below. A key to these five varietal taxa follows.

Key to Texas and Mexican varieties of *Monarda punctata*

1. Calyx lobes with outer surfaces conspicuously pubescent with white spreading hairs 0.5-1.5 mm long. (3)
1. Calyx lobes with outer surfaces and margins minutely hispidulous, w/o spreading white hairs. (2)
 2. Leaves strongly nervate, the nerves with mostly erect or ascending hairs; calyx lobes narrowly deltoid; Texas Gulf Coastal grassland regions from Cameron County (and possibly coastal northeastern México) northwards. var. *punctata*
 2. Leaves weakly nervate, the nerves with appressed or incurved hairs, or glabrate, calyx lobes broadly deltoid; southcentral Texas and closely adjacent México in red sandy soils. var. *correllii*

3. Undersurfaces of leaves pubescent along the lower veins with erect or ascending hairs 0.3-1.0 mm long; eastern and southern Texas.
..... var. *lasiodonta*
3. Undersurfaces of leaves pubescent with appressed or incurved hairs 0.1-0.2 mm long; northcentral and western Texas. (4)
 4. Calyx teeth narrowly acute, ca. 2 times as long as wide; northcentral Texas. var. *intermedia*
 4. Calyx teeth broadly acute, ca. as long as wide or nearly so; western Texas. var. *occidentalis*

11a. *MONARDA PUNCTATA* L. var. *PUNCTATA*

As indicated in the above account, this infraspecific taxon is confined to the Gulf Coastal regions of Texas and is readily recognized by its nonpilose narrowly deltoid calyx lobes and strongly nervate leaves. Inland it appears to grade into var. *correllii* B.L. Turner and var. *lasiodonta* A. Gray. Scora (1967) did not cite material of this taxon from Texas, apparently believing that its coastal distribution petered out in Louisiana, but I can not distinguish the Gulf Coastal material of Texas (Figure 7) from that of Louisiana and other Gulf states.

11b. *MONARDA PUNCTATA* L. var. *CORRELLII* B.L. Turner, var. nov. TYPE: U.S.A. Texas: Webb Co., red sandy soils along highway 83, 13 mi NW of Webb, 16 Jul 1957, D.S. Correll & I.M. Johnston 18109 (HOLOTYPE: LL!).

Monardae punctatae L. var. *punctatae* similis sed plantis robustioribus bracteis floralibus latioribus multo majoribusque dentibus calycis late deltoideis (1-2plo longioribus quam latioribus vs. 2-3plo) differt.

Suffruticose perennial herbs to 1 m high. Midstems with minute recurved arcuate hairs mostly 0.1-0.2 mm high. Corollas reportedly white or creamy-white. Calyx lobes triangular, similar to var. *lasiodonta* but completely void of long ciliate hairs. Nutlets brown, ovoid, glabrous, ca. 2.1 mm long, 0.6 mm wide.

REPRESENTATIVE SPECIMENS EXAMINED: U.S.A. TEXAS: (as arranged by county, west to east, beginning to the north): Val Verde Co.: *Cory 15234* (TEX). Medina Co.: *Barkley 13912* (TEX); *Johnston et al. 3423* (TEX).

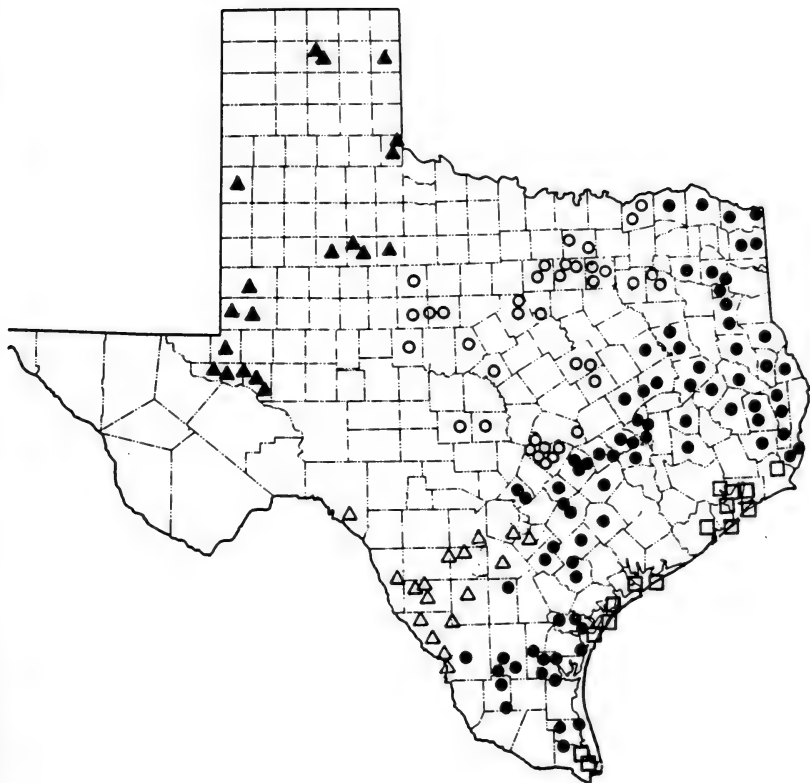


Figure 7. Distribution in Texas of *Monarda punctata* var. *correllii* (open triangles); var. *intermedia* (open circles); var. *lasiodonta* (closed circles); var. *occidentalis* (closed triangles); and var. *punctata* (open squares).

Bexar Co.: *Parks Rx 3132* (TEX). Maverick Co.: *Johnston et al. 3596* (TEX). Frio Co.: *Drews 29* (TEX); *Chavez 105* (LL); *Higdon 53-57* (TEX); *Tharp s.n.* (TEX). Wilson Co.: *Tejada s.n.* (TEX). Webb Co.: *Bruni 2* (LL); *Garcia 25* (TEX); *Perez 101* (TEX); *Ramírez 53* (TEX); *Rodríguez 82* (TEX). Atascosa Co.: *Fryzell 1296* (TEX). Karnes Co.: *Johnson 821* (TEX). Goliad Co.: *Williams 129* (TEX). Dimmit Co.: *Correll 20920* (LL). La Salle Co.: *Tharp 3712* (TEX). McMullen Co.: *Albers 49035* (TEX).

MEXICO. Tamaulipas: 6 mi S of Nuevo Laredo, *Barrera 149* (LL); 10 mi SE of Nuevo Laredo, *Rodríguez 84* (TEX).

This taxon is restricted to southcentral Texas and closely adjacent México. Previous workers have referred most of the plants which I have posited here to var. *coryi* (McClintock & Epling) Cory. I consider the latter to be a synonym of var. *lasiodonta*, which is readily distinguished from var. *correllii* by having pilose calyx lobes. The calyx lobes of var. *correllii* are quite similar to those of the coastal var. *punctata*, both lacking pilose hairs.

- 11c. *MONARDA PUNCTATA* L. var. *INTERMEDIA* (McClintock & Epling) Waterfall, *Rhodora* 52:38. 1950. BASIONYM: *Monarda punctata* L. subsp. *intermedia* McClintock & Epling, Univ. Calif. Publ. Bot. 20:184. 1942. TYPE: U.S.A. Texas: Van Zandt Co., near Wills Point, V.A. *Little 14456* (UC-UCLA!).

This taxon occurs in northcentral Texas (Figure 7), peripheral populations seemingly passing into var. *lasiodonta* in regions of near contact.

- 11d. *MONARDA PUNCTATA* L. var. *LASIODONTA* A. Gray, *Syn. Fl. N. Amer.* 2(1):375. 1878. BASIONYM: *Monarda lasiodonta* (A. Gray) Small, *Fl. S.E. U.S.* 1038, 1337. 1903. TYPE: U.S.A. Texas: w/o locality, 1834-35, *T. Drummond s.n.* (LECTOTYPE [selected by Scora 1967]: GH. Shinnery (1953) has given a detailed account of the presumed lectotype, this not mentioned by Scora in his treatment.

Monarda punctata L. subsp. *immaculata* Pennell, Bull. Torrey Bot. Club 46:187. 1919. *Monarda punctata* L. var. *immaculata* (Pennell) Scora, Univ. Calif. Publ. Bot. 41:47. 1967. TYPE: U.S.A. Texas: Victoria Co., Aloe, 8 Sep 1913, *Pennell 5494* (HOLOTYPE: PH; Isotype: NY!).

This, the earliest described Texas variety, was treated by McClintock & Epling (1942) as a questionable synonym of subsp. *villicaulis* Pennell, a taxon not occurring in Texas as treated here. Both Shinnery (1953) and Scora (1967)

recognized var. *lasiodonta* as a Texas endemic, although they both maintained var. *immaculata* as distinct, as do I.

- 11e. *MONARDA PUNCTATA* L. var. *OCCIDENTALIS* (Epling) Palmer & Steyermark, Ann. Missouri Bot. Gard. 22:634. 1935. BASIONYM: *Monarda punctata* L. subsp. *occidentalis* Epling, Madroño 3:25. 1935. TYPE: U.S.A. Oklahoma: Woods Co., Alva, Stevens 3072 (HOLOTYPE: NY!; Isotype: GH).

This variety occurs in northwestern Texas (Figure 7) and northwards and is relatively easily recognized, the more peripheral eastern populations showing little tendency to vary in the direction of its closest allopatric cohort, var. *intermedia*.

A single collection of this taxon has been examined from México, as follows: Chihuahua: near San Diego Hacienda, 25 Aug 1891, Hartman 730 (UC,US).

12. *MONARDA RUSSELIANA* Nutt. ex Sims, Bot. Mag. 511, t.2513. 1824. TYPE: U.S.A. Arkansas: grown in London from seeds collected near Fort Smith, w/o date, Nuttall s.n. (HOLOTYPE: BM, according to McClintock & Epling 1942).

This species is closely related to *Monarda bradburiana* Beck, which has a more northerly distribution. According to Scora (1967) these two species show evidence of intergradation in Oklahoma and elsewhere. Correll & Johnston (1970) accredit *M. bradburiana* to Texas, largely on the basis of a single unvouchered collection from Kerr County, Texas reported by McClintock & Epling (1942). Scora (1967), however, does not report having seen collections of the latter from Texas, nor have I.

13. *MONARDA STANFIELDII* Small, Fl. S.E. U.S. 1038, 1337. 1903. *Monarda punctata* L. var. *stanfieldii* (Small) Cory, Rhodora 38:407. 1936. *Monarda punctata* L. subsp. *stanfieldii* (Small) Epling, Madroño 3:25. 1935. TYPE: U.S.A. Texas: Hays Co.(?), "near San Marcos", w/o date, S.W. Stanfield s.n. (HOLOTYPE: NY!).

Monarda stanfieldii is a well-marked taxon largely confined to the granitic sands along the middle course of the Colorado River (Figure 5). McClintock & Epling (1942) recognized the taxon as a subspecies of *M. punctata*, while both Shinnars (1953) and Scora (1967) accepted its varietal status. I have found no suggestion that it intergrades with any element of *M. punctata*, in spite of its sympatry with that species (mainly var. *lasiodonta*).

14. *MONARDA VIRIDISSIMA* Correll, *Wrightia* 9:76. 1968. TYPE: U.S.A. Texas: Bastrop Co., 2 mi E of Bastrop along route 21, 10 Sep 1968, D.S. Correll 36368 (HOLOTYPE: LL!; Isotypes: GH, TEX!, UC!, US!).

This taxon was described subsequent to Scora's (1967) taxonomic study. Scora included collections of the taxon in his concept of *Monarda punctata* var. *lasiodonta*.

Monarda viridissima is a fall-flowering taxon known by numerous collections, these largely confined to outcrops of Carrizo sands in central Texas (Figure 6) where it grows with or near *M. punctata* (e.g., Albers s.n., 23 Jun 1932, TEX, both taxa mounted on the same sheet) without signs of intergradation, although the occasional hybrid between these might be expected.

Correll & Johnston (1970) took *Monarda punctata* var. *immaculata* to be a synonym of *M. viridissima*, but examination of the type of the former (from Goliad Co., Texas) shows it to be synonymous with *M. p.* var. *lasiodonta*, which was recognized by Correll & Johnston.

I visited the type locality of *Monarda viridissima* in early September of 1994 and could not find individuals of the taxon (the once single lane road now transformed into a 4-lane highway). However, at a site ca. 1/2 mi west of the type locality (along County Road 118 west off of Highway 21), I located a small population of 30-40 plants of *M. viridissima*. The individuals were well-scattered and just coming into flower (Turner 94-114). All of the plants were essentially alike as to leaf shape, size, and vestiture. No plants of *M. punctata* were found growing anywhere in the vicinity of the population concerned.

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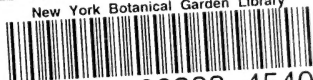
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